1-1-2013

Bamboo Nutritional Composition, Biomass Production, and Palatability to Giant Pandas: Disturbance and Temporal Effects

Jennifer L. Parsons

Bamboo nutritional composition, biomass production, and palatability to giant pandas: disturbance and temporal effects

By

Jennifer L. Parsons

A Dissertation
Submitted to the Faculty of
Mississippi State University
in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy
in Agricultural Sciences (Animal Nutrition)
in the Department of Animal and Dairy Sciences

Mississippi State, Mississippi

August 2013

Bamboo nutritional composition, biomass production, and palatability to giant pandas: disturbance and temporal effects

By

Jennifer L. Parsons

Approved:

_____	_____
Brian J. Rude Professor and Graduate Coordinator Animal and Dairy Sciences (Major Professor)	Brian S. Baldwin Professor Plant and Soil Sciences (Committee Member)
_____	_____
Stephen Demarais Professor Wildlife, Fisheries, and Aquaculture (Committee Member)	Gary N. Ervin Professor Biological Sciences (Committee Member)
_____	_____
Francisco Vilella Assistant Unit Leader Cooperative Fish and Wildlife Research Unit (Committee Participant)	George M. Hopper Dean of the College of Agriculture and Life Sciences

Name: Jennifer L. Parsons

Date of Degree: August 17, 2013

Institution: Mississippi State University

Major Field: Agricultural Sciences (Animal Nutrition)

Major Professor: Brian J. Rude

Title of Study: Bamboo nutritional composition, biomass production, and palatability to giant pandas: disturbance and temporal effects

Pages in Study: 208

Candidate for Degree of Doctor of Philosophy

The giant panda (*Ailuropoda melanoleuca*) subsists on bamboo, but lacks gastrointestinal modifications for fiber digestion. Pandas display dietary selectivity for certain plant parts; however, cues for selection are unknown, and few have examined panda feeding behavior and bamboo nutrient composition simultaneously. Bamboos are clonal plants, with seasonal cycles of nutrient accumulation related to peak photosynthesis and recruitment. These cycles can be destabilized by aboveground disturbance; however, effects of disturbance on nutritional quality and sustainability of bamboo for primary consumers have not been studied. I examined 4 factors that may contribute to bamboo nutritional quality or sustainable harvest: season, ramet maturity and age, and disturbance. I conducted a 3-year study with *Phyllostachys aureosulcata* (PLLAU), *P. glauca* (PLLGL), and *P. rubromarginata* (PLLRU), at the Shelby County AgriCenter, Memphis TN, applying 3 disturbance treatments in a replicated split-plot design: control, 3% and 20% annual removal of biomass. Bamboo was sampled 8 times/year and divided into shoot, leaf, and culm (central stem) for analysis of crude protein (CP), neutral- and acid-detergent fiber (NDF and ADF), ash, lipid, minerals, and

acid-insoluble ash (AIA). I quantified bamboo-stand production, maturity, recruitment and mortality. Biomass removed from PLLAU was used in diet-selection trials with 2 giant pandas, observing consumption of plant parts and bamboo from different disturbance treatments, and sampling bamboo for allelochemical and starch analysis. Disturbance effects were evident only for branch and culm dry mass in PLLRU. In Year 2, drought conditions and peak roosting blackbird populations confounded results. Defoliation and guano deposition preceded changes to soil chemistry, bamboo composition, and stand structure; recruitment increased for PLLRU. After accounting for confounding factors, less-mature bamboo had greater concentrations of most nutrients, but less NDF, ADF, and K. Two-year-old ramets had greater CP, NDF, lipid, P, K, S, and Cu, but less Ca and Fe, than 1-year-old ramets. I confirmed seasonal plant-part selection by pandas, but found no correlation between leaf consumption and AIA concentration. Culm starch analyses were insufficient to establish a clear pattern. I recommend further investigation of non-structural carbohydrates in bamboo, and palatability testing of undisturbed versus disturbed bamboo, which I was unable to examine.

DEDICATION

To my husband, who has not only been an unfailing source of support and motivation, but has also served as lab assistant, sounding board, counselor, and massage therapist, and singlehandedly kept me from starving when I would not have otherwise stopped to eat. To my parents, for teaching me from a young age that I could do anything I made up my mind to do, and for constantly reinforcing that idea throughout my life. To my grandmother and aunts, who I have always considered role models of successful, grounded, happy, and self-assured women.

ACKNOWLEDGEMENTS

I wish to thank my collaborators on this study: Brian Rude, Brian Baldwin, Meghan Carr, John Ouellette, and Heidi Bissell, as well as the financial support of Ocean Park Conservation Foundation (Hong Kong), the Memphis Zoo, and Mississippi State University. This work would not have been possible without the invaluable assistance of Cathy Aultman and the H. W. Essig Nutrition Laboratory; Barbara Myers, Jennifer Bernard, Rachel Wostl, Carolyn Apanavicius, and the Conservation and Research, Mammal, and Horticulture Departments at the Memphis Zoo; Daniel Ballhorn, Department of Plant Biology, University of Minnesota; Robert Sikes and Tommy Finley, Department of Biology, University of Arkansas – Little Rock; Adam Orr, Department of Animal and Dairy Sciences, Mississippi State University; Joe Deraney and Lexi Steinweg-Woods, University of Wisconsin – Madison; the laboratory of Mary Beth Hall, U.S. Dairy Forage Research Center and University of Wisconsin – Madison; Lance Miller, Institute for Conservation Research, San Diego Zoo Global; and volunteers and interns from Mississippi State University, Rhodes College, the University of Memphis, and Christian Brothers University, in particular Mandy Lawson, Tracey Boler, Katelyn Armstrong Allender, Alisha and Frankie Hollander, and Casey and Chris Asa.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

Background

The giant panda (*Ailuropoda melanoleuca*; Carnivora, Ursidae; Chorn and Hoffmann 1978) is one of the most critically endangered animals in the world. According to recent estimates, between 1100 and 1600 individuals remain in the wild (WWF 2004). Giant pandas also possess a unique evolutionary history. Although general consensus among taxonomists places them among bears (Gittleman 1999), the giant panda was the first of the extant ursids to diverge from a common ancestor, and over the intervening millennia has adopted a lifestyle of almost exclusive herbivory. So extreme is the species' dietary specialization that between 95 and 99% of the diet of wild pandas consists of one feed item: bamboo (Poaceae, Bambusoideae, Bambuseae; Chapman 1997; Schaller et al. 1985; Edwards et al. 2006). This juxtaposition between their carnivorous evolutionary past and herbivorous present has placed the species in an interesting position with regard to its ecology and conservation, particularly concerning its nutritional ecology and habitat management.

The current habitat of the giant panda is located in the Liang, Xiangling, Qionglai, Min, and Qinling mountains of central China (Sichuan, Shaanxi, and Gansu provinces), at an elevation of 1200 to 3500 m (Schaller et al. 1985). This represents a severe constriction of their original distribution; at one point, giant pandas ranged through much

of eastern China and the northern regions of southeast Asia, down to an elevation of 500 m (Schaller et al. 1985). Giant pandas are typically found in steep mountainous terrain, within subalpine coniferous forests, with fir, spruce or pine overstory, some broad-leafs (birch, maple, cherry) and bamboo or rhododendron understory (Schaller et al. 1985). Because large trees provide important den sites, particularly key for reproductive females (Schaller et al. 1985), pandas depend on both aspects of their habitat – old-growth overstory for shelter, and bamboo understory for food.

In late spring and early autumn, pandas undergo altitudinal migrations between winter and summer ranges (Long et al. 2004; Wang 2003). Because bamboo species in these mountains are often exclusive to particular elevations, seasonal movements are accompanied by a dietary staple shift. In the Qionglai mountains of Wolong Natural Reserve, for example, pandas shift between a winter diet of *Fargesia robusta*, which grows from 1600 to 2800 m, and a summer diet of *Bashania fangiana*, found from 2600 to 3500 m (Reid and Hu 1991). Wild pandas in other locations follow suit, always oscillating between *Fargesia* spp. at lower altitudes and *Bashania* spp. at higher elevations (Schaller et al. 1985, Wang et al. 2007). Thus, the diet of wild pandas is restricted to a handful of temperate woody bamboos, which grow under a narrow range of environmental conditions. The challenge of keeping giant pandas in captivity is to attempt to duplicate the nutritional quality of their natural diet using alternate bamboo species that can be readily grown in a wide variety of conditions.

Millennia of evolutionary pressures have introduced a number of skeletal modifications that suit giant pandas to their peculiar diet. Enlarged masseter muscles for chewing woody plant tissues are accommodated by wide, flaring zygomatic arches, a

large sagittal crest, and deep temporal fossae (Schaller et al. 1985). The teeth are substantially altered from typical bear dentition, with large, broad molars and premolars for grinding and reduced carnassials (Bleijenberg and Nijboer 1989). Although the canines do not differ substantially from those of other bears, giant pandas use them to help break apart and peel woody stems of bamboo while feeding. The most striking skeletal change is in the carpal bones of the forepaws, where the radial sesamoid has developed a projection or "pseudothumb," to enable gripping and manipulation of feed items (Schaller et al. 1985; Edwards et al. 2006).

The same degree of modification, however, has not occurred in the digestive tract. Giant pandas retain the simple gastrointestinal tract of their carnivore ancestors, with no apparent specialized organs to accommodate the digestion of vegetative matter (Bleijenberg and Nijboer 1989, Dierenfeld 1997, Hunter et al. 2003; Edwards et al. 2006). Most herbivore specialists have a functional compartment or outpouching, either before the glandular stomach or in the hindgut, to house large pools of symbiotic microbes that enable the breakdown of cellulose in plant cell walls. Herbivores also tend to have elongated intestines to increase retention time and enable maximum absorption of nutrients (Pond et al. 1995). The ratio of intestinal tract length to body length in giant pandas is less than that of dogs and only slightly more than felids, which are obligate carnivores (Bleijenberg and Nijboer 1989). There is no evidence of any compartments to house cellulolytic microorganisms (Bleijenberg and Nijboer 1989, Dierenfeld 1997, Hunter et al. 2003). Pandas also have extremely short digesta retention times (4 to 10 hours; Dierenfeld 1997; MZS 2006; Sims et al. 2007), and one of the smallest digestive capacities of all mammalian herbivores (10 to 40%; Schaller et al. 1985; Long et al.

2004; Edwards et al. 2006; Sims et al. 2007). Although the large intestine does exhibit traits of microbial colonization (e.g., enlarged surface area, microbes isolated from fecal boluses; Hirayama et al. 1989; Edwards et al. 2006), these passage rates would make significant hindgut fermentation impossible.

In light of the limitations of their digestive tract, giant pandas must employ three strategies in order to meet daily nutritional needs: 1) energy conservation, 2) maximal intake, and 3) extreme dietary selection. Pandas are adept at conserving their scant dietary energy by minimizing all non-feeding activity: in captive pandas, 20 to 30% of daylight hours were spent feeding, 50 to 55% resting, and 10 to 15% on all other activities (MZS 2006). In the wild, in a 24-hour period, 55% of time was spent feeding, 41% resting, and 4% on all other activities (Schaller et al. 1985). When resting, giant pandas often enter a form of deep sleep that closely resembles daily torpor, a form of metabolic shutdown often used for energy conservation by many species of small mammals and birds.

Giant pandas consume massive quantities of bamboo. Whereas typical daily dry-matter intake for mammalian herbivores of similar body size is 1 to 3% of body mass (Robbins 1993), captive pandas commonly ingest 2 to 6% of body mass as dry matter (Edwards et al. 2006). That prior studies on captive individuals always included a proportion of highly digestible non-bamboo items (Dierenfeld et al. 1982; Mainka et al. 1989; Nickley 2001) makes these numbers all the more impressive. In the wild, without these more-digestible dietary supplements, dry matter intake is between 4 and 10% of body mass. Our recent data on captive populations indicate that, on a bamboo-only diet, a single giant panda can eat as much as 30 kg of bamboo per day (Sims et al. 2007). This

adds up to almost a metric ton of bamboo per month, or 12 metric tons in a year, and represents a significant investment in procurement of materials on the part of zoological institutions. These intake rates also mean that free-ranging individuals must maintain large, often-exclusive home ranges (e.g., 4 to 6 km^2; Schaller et al. 1985) to ensure consistent availability of sufficient forage. Indeed, many aspects of the giant panda's natural history and behavior (e.g., solitary existence, short estrus period, brief gestation, altricial young with a long rearing period, very low reproductive rate) are dictated by the nutritional ecology of a species wholly dependent on this single, poorly-assimilated food source (Schaller et al. 1985; Edwards et al. 2006).

Giant pandas also exhibit extreme dietary selectivity, increasing efficiency of nutrient intake by consuming only certain pieces of bamboo that are presumably greater in nutritional value. This selection applies to species consumed as well as parts of the plant, with branches largely ignored and consumption of leaves or the central woody stem (culm) depending on time of year (Dierenfeld 1997). Their degree of specificity is so notable that captive pandas have been known to refuse as much as 50% of bamboo offered (MZS 2005; Sims et al. 2007; this study). To further complicate attempts to predict feeding behavior, bamboo-species and plant-part selection are not static: within a given year, diet selection changes constantly but consistently, representing a specific but moving target for researchers seeking to understand the nutritional ecology of the species.

The nature of giant pandas' selective herbivory was the topic of behavioral research with two pandas at the Memphis Zoo during the two years prior to initiation of this study, and preliminary data indicated a consistent annual pattern. Both individuals underwent major shifts in bamboo species consumed over the course of the year,

particularly in early February and late May (MZS 2004). They also showed a regular pattern in plant part selection, consuming mainly leaf matter from June to December, transitioning during January and February to a predominantly culm diet in March, April and May, consuming a large amount of shoots when they are available in May, and then suddenly switching back to a mostly-leaf diet by the beginning of June (MZS 2006). Although the specifics differ by location, this general pattern is consistent with patterns of bamboo species and plant-part selection by giant pandas in other zoos (Dierenfeld 1997; Tarou et al., 2005; Sims et al. 2007). The underlying cause of such seasonal diet shifts is unknown, but presumably the animals are responding to either changes in bamboo or circannual rhythms within the pandas themselves. These results also appear to echo the seasonal foraging behavior of wild pandas and their semiannual shift between foraging sites and therefore bamboo species availability. A changeover from a leaf to culm diet has also been observed in wild pandas during winter months, as well as selection for fresh shoots in May and June (Schaller et al. 1985; Reid and Hu 1991; Dierenfeld 1997). In captivity, plant-part shifts can occur even when consuming the same species of bamboo year-round (MZS 2006).

Because the sensory or physiological cues driving diet selection in giant pandas are poorly understood, because a better understanding of these cues would greatly improve captive and free-ranging animal management, and because few prior studies had examined these questions from both forage-utilization and plant-physiology perspectives, I undertook the present study. The genesis of this project lay in a series of communications with giant panda managers at Ocean Park Hong Kong, who reported that their pair of captive pandas had begun to avoid bamboo cut from the same stand(s) after

at least 6 years of harvesting without problems (J. Tang, Ocean Park Hong Kong, personal communication). Our hypothesis at the time was that disturbance in the form of harvest pressure may be interacting with particular aspects of bamboo physiology and life history to alter the biochemistry or age-class distribution of remaining vegetation in undesirable ways, making it unpalatable to the animals. However, no prior studies had examined either bamboo biochemistry or bamboo life history in this sort of disturbance context, particularly with an eye toward mammalian herbivory. I sought to improve our understanding of bamboo life-history and physiology in managed situations, to ideally prevent this sort of problem in other zoological institutions.

Like the giant panda, bamboos are an interesting evolutionary paradox. All bamboos are grasses, monocotyledonous members of subfamily Bambusoideae, family Poaceae or Gramineae (the "true" or broad-leaved grasses; Clark 2006). However, bamboos used as forage, both by free-ranging animal populations as well as in captive situations, often share traits with trees and shrubs, rather than herbaceous members of their own family. Bamboos do share certain traits with other grasses, namely: 1) hollow stems called culms, sectioned at intervals by leaf- or branch-bearing nodes, 2) the prominence of silica phytoliths, 3) flowers arranged in spikelets, each of which contains one or more florets, and 4) the ability to reproduce by means of vegetative propagation (McClure 1966; Clark 2006). This last trait has significant implications for life history and resource utilization, as I will discuss later. The most recognizable traits which distinguish Bambusoideae from other graminoids include 1) woody culms with substantial branching, and 2) the structural and functional prominence of belowground rhizome systems (McClure 1966). This is particularly true for tribes Bambuseae and

Arundinarieae, the woody bamboos, as opposed to Olyreae, the herbaceous bamboos (Clark 2006).

Bamboos of genus *Phyllostachys*, *Pseudosasa*, *Bashania*, *Fargesia*, and *Bambusa* are of particular interest to zoological institutions, as these genera comprise the majority of bamboo offered to captive populations of giant pandas and other temperate bamboo specialists (Edwards et al. 2006). These bamboos are subject to widespread commercial cultivation, and grow in most climates in the United States, Europe, and Asia. Kleinhenz and Midmore (2001) call *Phyllostachys pubescens* "the world's single most important bamboo species", covering 30% of bamboo forests (over 2 million ha) in China alone. *Phyllostachys* and *Bambusa* spp. are perhaps the most familiar of bamboos to the general public: both are used heavily as ornamental vegetation in botanical and zoological gardens, and the iconic multistory, seemingly-endless bamboo forests of China, often depicted in film and photographs, are typically made up of *Phyllostachys* spp. The majority of cultivated stands are of course used as timber, however both genera are also grown as forage for pandas and other species in many locations worldwide (Edwards et al. 2006). There is a single genus of native bamboo in the United States, *Arundinaria*, and especially in the Southeast, rivercane or giant cane (*Arundinaria gigantea*) was until recently used for animal forage (personal observation; R. Daujotas, Zoo Atlanta, personal communication). However, the once-extensive canebreaks that typified this region have almost all been cleared for agriculture in the past 200 years (McClure 1966), and are now considered a critically endangered ecosystem (USDA 2012).

When feeding giant pandas in captivity, two things are important to keep in mind. First, because of the considerable differences in climate between free-ranging panda

habitat and most zoological institutions, we are almost universally forced to manage pandas using alternate bamboo species than those they would consume in the wild. Bamboo species found in the mountains of China are cold-adapted, shade-loving, and dependent on complex forest structure (Schaller et al. 1985), as opposed to the monoculture plots typical of cultivation for animal forage. Thus, these bamboos are generally ill-suited to commercial cultivation, and the closest many institutions can hope to come is to use bamboos of the same genera (*Bashania* and *Fargesia*), though almost never the same species. Supplementation with additional genera is always necessary to provide sufficient and consistent supplies of forage material year-round (Edwards et al. 2006). Second, we must keep in mind that feeding bamboo to giant pandas that is cut and transported from sometimes large distances (as much as 150 kilometers for some institutions; personal observation) does not duplicate the same nutritional environment they would experience if foraging among fresh bamboo still growing from the ground. At the moment vegetation is clipped, particularly in leaves, ongoing cellular respiration rapidly converts soluble sugars and other volatile cell solubles to gaseous or other compounds, altering energy density and nutritional composition (Hopkins and Huner 2004). For both of these reasons, captive animal managers commonly supplement panda diets with nutritionally-complete items that will correct any energy or micronutrient imbalances compared to nutrient intake of wild pandas – often in the form of a commercial high-fiber primate biscuit (personal observation). I therefore recognize from the outset that this study does not duplicate the habitat or nutritional environment of wild giant pandas. However, certain aspects of life-history and physiology are common to all

bamboos and all giant pandas, regardless of their location. It is hoped that this study will serve as a good model of these processes in multiple species of temperate bamboos.

One of the more notable features of woody bamboos is their ability to propagate rapidly and thrive in many habitats. Both are central features of clonal plants. The phenomenon of self-cloning has arisen multiple times in the plant kingdom, and is defined as "asexual, vegetative production of offspring individuals, which are genetically identical … to each other and to the parent plant. … [O]ffspring individuals are produced from somatic tissue without passing through regular meiotic cell cycles, thereby by-passing sexual recombination of the genetic material." (Stuefer et al. 2002, p. 1). In woody bamboos, this is achieved through the production of underground structures that give rise to individual aboveground units called ramets. A group of interconnected ramets is called a genet, or simply a clone. Two forms of vegetative propagation exist, both represented among bamboos: 1) "clumping" or pachymorphic species, in which underground structures called tillers arise from the parent plant and give rise to closely-spaced ramets, and 2) "running" or leptomorphic species, in which underground connections are called rhizomes and can be quite long, giving rise to potentially widely-spaced ramets (McClure 1966; Recht and Wetterwald 1996; Kleinhenz and Midmore 2001).

Clonality conveys distinct advantages with regard to survival, recruitment, and resource utilization. The maintenance of physical connections among ramets allows for the ability to act as a single functional organism. Physiological integration allows for colony-level responses to stimuli through hormone signaling, as well as sharing of resources among ramets, and thus maximal exploitation of heterogeneous environments

(Stuefer et al. 2002). The capacity for lateral rhizomatous extension also means that the genet is not stationary: it can expand its radius (sometimes selectively), allowing it to adapt to changes in resource availability through time or space by quickly projecting new growth into uncolonized soil (Piqueras et al. 1999).

Because of this reliance on belowground lateral expansion, woody clonal plants often exhibit a particular pattern of recruitment, growth, and nutrient flux. Reproduction commonly occurs in spring, just before the period of maximum sunlight intensity in early summer (Kleinhenz and Midmore 2001). Prior to the shooting season, bud formation occurs at belowground rhizomal nodes. Before each forming shoot emerges from the ground, a number of highly compressed culm sections are already in place, with a pre-determined number of internodes (Recht and Wetterwald 1996). Cell division takes place at the apex, which lies under a fibrous sheath that covers the entire shoot. The timing of shoot emergence is regulated by soil temperature, dicatated by each bamboo species' natural history. Upon reaching this critical temperature, shooting occurs in a burst of rapid growth within a narrow span of time, as pre-formed internodes elongate quickly under osmotic pressure (Recht and Wetterwald 1996; Hopkins and Huner 2004). Bamboo shoots elongate quite rapidly, sometimes growing from emergence to full height within a matter of days. Shoot emergence for an entire stand is sometimes completed within 2 to 3 weeks; maximum shoot elongation, shedding of the outer sheath, and exposure of branches (called jointing) can occur within 1 to 2 weeks of shoot emergence (this study).

A flush of leaf growth follows jointing, with upregulation of photosynthetic enzyme systems through the length of summer (Kleinhenz and Midmore 2001). As

available sunlight wanes in autumn and winter, leaves senesce but do not all die; only the oldest leaves are shed and the stand remains otherwise evergreen (Li et al. 1998 a,b; Kleinhenz and Midmore 2001). In late winter, upregulation of belowground tissues occurs, in preparation for the next bout of shoot production. It is important to note that growth is generally determinate in woody bamboos: after jointing, each ramet has reached its maximum height and culm diameter, and the only cellular proliferation that occurs after this point is in production and replacement of leaf tissues, and the maintenance and fortification of existing structures (Young 1991).

Throughout this annual cycle, clonal species also experience a predictable pattern of nutrient accumulation and flux. Clonal plants demonstrate a strong seasonal effect in particular on the amount of carbohydrate accumulation and storage, as well as the form of carbohydrate accretion (sugars vs. starches; Zasada et al. 1994; Landhausser and Lieffers 1997, 2002; Li et al. 1998a). There is also a difference by plant part and growth stage in the accumulation and storage of total non-structural carbohydrate (TNC) and other nutrients (Li et al. 1998a). In clonal shrubs and trees, stored starches from the root system are mobilized in spring to support new growth, followed by an accumulation of sugars and proteins in the leaf canopy with increased photosynthetic capacity during the growing season. With the onset of autumn senescence, soluble sugars from aboveground organs are converted back to stored starches in the roots and rhizomes (Zasada et al. 1994; Landhausser and Lieffers 1997, 2002). Because aboveground recruitment in clonal species depends on nutrient reserves in below-ground structures, this cycle of nutrient shunting is important to the maintenance of the stand, and a linear quantitative relationship between root stores and new shoots or suckers has been shown in multiple

species (Zasada et al. 1994, Landhausser and Lieffers 1997, 2002). Carbohydrate and nutrient dynamics in bamboos seem to follow along the same lines as those of other woody clonal species (Li et al. 1998a). Although the evergreen nature of bamboo reduces the need to support a spring leaf flush, the phenomenon of rapid shooting and elongation of multiple culms within a few weeks' time places the same demands on nutrient stores. Because the season of active shoot growth corresponds with a time when senescence occurs in the oldest leaves, photosynthetic capacity is reduced and new ramets must rely even more on stored nutrients for growth (Li et al. 1998a).

Leptomorphic bamboos in particular also demonstrate distinct cyclicity in leaf turnover. Individual leaves normally have a lifespan of 2 years, and are shed late in their second winter, just before shooting (Kleinhenz and Midmore 2001). The period of maximal photosynthetic capacity occurs during the first year, with more TNC and other nutrients present than in second-year leaves (Li et al. 1998a). Thus, leaf-age structure becomes particularly important: in a stand that is balanced with respect to 1-year-old versus 2-year-old leaves, year-to-year photoassimilate production remains relatively stable – typical of mature, established stands. In younger stands, all leaves may be of the same age, and may experience a multi-annual cycle of leaf shedding, leaf density, and average leaf maturity (Li et al. 1998 a,b), and consequently rates of carbon fixation may be more heterogeneous among years, and nutritional quality of an entire leaf canopy could vary widely.

Aside from unique patterns of clonal nutrient cycling, two other prominent features of bamboos may affect forage quality. Both may potentially influence forage palatability, but it is as yet unknown whether either have any bearing on giant panda

herbivory or diet selection. The first is the prominent role of biogenic silica in bamboo structures; the second is the potential for chemical defense against herbivory.

Many plants, particularly those in the grass family, use biogenic silica in addition to fiber to reinforce their structure . Soluble silicic acid is taken up from the soil, modified to amorphous hydrated silica or silica gel ($SiO_2 \cdot nH_2O$) and, in bamboos, deposited in the internal layers of the cell wall (Kaufman et al. 1981, Sangster and Parry 1981, Motomura et al. 2002). Bamboos are notorious for large amounts of silica, even among grasses—presumably because of their long lifespan for a monocot, and subsequent ability to accumulate silica over time. There also seems to be a role for silica in improving culm mechanical properties (Kleinhenz and Midmore, 2001); perhaps bamboos have a particular need for silica-assisted structural support because of the heights to which they are capable of growing.

Silica deposition varies widely by plant part, with the greatest concentrations detected in the leaves (up to 41% in *Sasa* spp.; Motomura et al. 2002). Amounts of silica in bamboo leaves have also been shown to increase up to 3-fold with season, age, and maturity (especially in the 3 to 4 months following emergence); the perennial nature of bamboos relative to other grasses may in part explain their ability to accumulate such large concentrations (Motomura et al. 2002, 2004). Bamboo samples from the Memphis Zoo reflect the differences by plant part reported in the literature. Analyses of 125 samples of *Phyllostachys* spp. taken between May 2003 and May 2004 found that ash or mineral comprised 10.98 ± 2.03% (max. 18.21%) of leaf samples, but only 1.99 ± 0.83% (max. 6.15%) of culm. The majority of ash in bamboo samples is probably silicate

(Greenway et al. 1999); thus these measurements may be interpreted as indices of silica concentration in *Phyllostachys*.

Silica may decrease digestibility by inhibiting microbial access to cell wall carbohydrates, and may have a negative impact on palatability (Greenway 1999). Aside from tooth wear, potential health risks include siliceous phytoliths or stones in the kidney or bladder (Greenway 1999). Kleinhenz and Midmore, (2001) note that addition of soil Si in commercial cultivation should only occur in timber stands, as it may reduce quality of edible shoots by increasing fiber concentration. Despite such repercussions, the effect of large or varying concentrations of silica on herbivores such as the giant panda has yet to be examined in detail. However, Schaller et al. (1985) reported a correlation between seasonal increases in bamboo leaf silicification and conversion of wild pandas from a diet of leaves to culm. Although this association does not infer a cause and effect relationship, nor does it indicate whether pandas can detect silica in plant tissues, greater amounts of silica may affect nutritional composition through simple dilution, and could likewise affect the taste of forages. Despite the lack of information on how biogenic silica affects herbivores, the converse has been examined. McNaughton et al. (1985) found that in African grasses, silicification increased as a response to defoliation and was greater in plants from heavily grazed areas, indicating a possible role for silica as a defense against herbivory.

Most monocots rely little on plant defensive compounds, otherwise known as allelochemicals, to deter herbivory (Herms and Mattson 1992). The only published accounts of antiherbivore defenses in bamboos are among tropical species in Madagascar (e.g., *Cephalostachyum* spp. and *Cathariostachys madagascariensis*) – however these

reports are of note. Tissues in some of these bamboos contain considerable amounts of cyanogenic glycosides that rapidly convert to hydrogen cyanide when masticated (Glander et al. 1989, Tan 1999). Bamboo lemurs (genus *Hapalemur*) are specialist feeders on tropical bamboos, and through selective consumption of low-fiber portions and new growth, *H. aureus* may ingest a daily average of 80 mg of cyanide during certain times of the year (Glander et al. 1989). This amount is approximately equal to 12 times the human lethal dose; fortunately, *Hapalemur* spp. are remarkably resistant to the effects of cyanide toxicity. There are, however, no published reports in which temperate bamboos have been tested for this compound. Furthermore, Liese and Weiner (1997) did find production of unspecified phenolic compounds in response to wounding in several genera of temperate bamboos, along with lignification of damaged tissues. Whether these findings represented the production of tannins is unknown, and again has yet to be tested in temperate bamboo species.

Justification and objectives

Procurement of bamboo represents the greatest cost for institutions housing giant pandas. Mismanagement of a bamboo stand over the long term could result in lower palatability, wasted bamboo, and wasted money and effort. At the same time, captive animal managers must find a way to propagate, manage, and harvest bamboo in such a manner that quantity, quality, and diversity are all optimized. The greatest single concern for wild panda conservation is management of native habitat. Land clearing in or near wild panda reserves, even on a small scale, could affect surrounding habitat. Thus, information on the complexities of bamboo biochemistry is important not only to captive animal institutions, but also to managers of wild panda habitat, faced with a difficult

balance between the needs of animal and human populations. Proper understanding of factors that affect bamboo composition and physiology, as well as the manner in which pandas respond to intrinsic changes in bamboo, is essential.

I undertook a study that focused on the most fundamental influences on bamboo quality: season, age class, and stage of growth. I also examined the effects of disturbance and disturbance intensity on the biochemical composition of bamboo as it may affect palatability to giant pandas. In addition to laboratory analyses, this study included behavioral trials in conjunction with researchers from the Memphis Zoo, to directly observe panda-bamboo interactions through time under different disturbance regimes, while simultaneously quantifying potential chemical cues for dietary selection. Finally, in order to inform sustainable bamboo management practices, I quantified colony-level growth and structure of bamboo stands to moderate or more intense disturbance. The intention of this study was to provide background on basic bamboo physiology and panda diet selection that will help institutions manage resources effectively, while targeting animals' changing nutritional needs. More importantly, I hoped to enhance decisions aimed at improving the nutritional environment for pandas in the wild, to further the preservation of the species as a whole.

The specific objectives of this study were as follows: 1) Quantify the effects of season, age class, stage of growth, and harvest pressure on the nutritional composition of bamboo; 2) Test for the presence or absence of specific secondary metabolites in temperate bamboos; 3) Identify compounds in bamboo that may serve as cues for diet selection by giant pandas; 4) Examine alterations to diet selection by pandas that may result from differences in bamboo harvest intensity; 5) Quantify environmental factors

and life-history traits that affect biomass production and availability in bamboo stands cultivated for forage; and 6) Determine whether and how aboveground disturbance affects bamboo production, with the goal of identifying a sustainable rate of biomass removal.

Format

This study is presented in three chapters, each formatted for manuscript submission to peer-reviewed journals:

- Chapter 2, *Nutritional quality of bamboo for a specialist forager: influence of season, bamboo maturity and age, and disturbance*: formatted for Grass and Forage Science.
- Chapter 3, *Recruitment, mortality and biomass production of Phyllostachys bamboos: toward sustainable aboveground disturbance*: formatted for Plant Ecology
- Chapter 4, *Impact of season and bamboo disturbance on giant panda feeding behavior*: formatted for Zoo Biology

CHAPTER II

NUTRITIONAL QUALITY OF BAMBOO FOR A SPECIALIST FORAGER: INFLUENCE OF SEASON, BAMBOO MATURITY AND AGE, AND DISTURBANCE

Abstract

A number of endangered species depend on bamboo as a primary food source, including the giant panda. We sought to quantify 4 factors that contribute to nutritional quality of bamboo as a forage for this and other primary consumers: season, ramet maturity and age, and degree of aboveground disturbance. Over 2 years, we sampled bamboo from 3 *Phyllostachys* species in a replicated split-plot design, dividing samples into shoot, leaf, and culm (central stem), and analyzing for crude protein (CP), neutral- and acid-detergent fiber (NDF and ADF), ash, lipid, and minerals. Seasonal differences were detected, but differed year to year and were confounded by peak populations of native blackbirds in winter 2006 to 2007. Young shoots had the greatest concentrations of all nutrients except fiber, and increased in NDF and ADF and decreased in all other nutrients as shoots elongated. Leaves increased in ash, Ca, Fe, Mn, and Zn as they matured, and decreased in K. Maturing culm increased in CP, P, Fe, and Zn, and decreased in ash. Compared to 1-yr-old ramets, 2-yr-old ramets had greater concentrations of CP, NDF, lipid, P, K, S, and Cu. One-yr-old ramets had greater Ca and Fe concentrations. We did not detect biologically significant effects of disturbance on

nutritional composition. Although we were not able to analyze non-structural carbohydrates, we propose that such easily-digestible nutrients represent an important energy source for pandas, and are potentially affected by the variables investigated in this study.

Introduction

Woody bamboos (Poaceae: Bambusoideae; Chapman, 1997) share many characteristics of both graminoids and clonal trees and shrubs. All members of Bambuseae (tropical woody bamboos) and Arundinarieae (temperate woody bamboos) display gregarious monocarpy, producing seeds as a clonal unit just before death of the entire clone. Throughout the rest of a clone's lifetime, reproduction proceeds exclusively through vegetative propagation (Keeley and Bond, 1999). As such, bamboos follow a circannual pattern typical of most clonal species. During peak photosynthesis (typically summer in temperate zones), physiological processes are upregulated in leaf tissues. As available sunlight wanes in autumn and winter, leaves senesce but do not all die; only the oldest leaves are shed and the stand remains otherwise evergreen. In late winter, upregulation of belowground tissues occurs, in preparation for shoot production. In spring, shoot emergence and elongation occurs in a burst of growth within a narrow span of time, typically triggered by a key soil temperature corresponding to each species' natural history. Shoot emergence for an entire stand is often completed within 2 to 3 weeks; maximum shoot elongation, shedding of the outer sheath, and exposure of branches (called jointing) occurs within 1 to 2 weeks of shoot emergence. A flush of leaf growth follows, on new ramets as well as pre-existing ramets (to replace winter shed),

and peak photosynthesis begins again (Tripathi and Singh, 1994; Shanmughavel and Francis, 1996, 2001; Li *et al*., 1998a,b; Wang *et al*., 2007).

Throughout this annual cycle, clonal species also experience a predictable pattern of nutrient accumulation and flux. Clonal plants demonstrate a strong seasonal effect in particular on the amount of carbohydrate accumulation and storage, as well as the form of carbohydrate accretion (sugars vs. starches; Zasada *et al*., 1994; Landhausser and Lieffers, 1997, 2002; Li *et al*., 1998a). There is also a difference by plant part and growth stage in the accumulation and storage of total non-structural carbohydrate (TNC) and other nutrients (Li *et al*., 1998a). In clonal shrubs and trees, stored starches from the root system are mobilized in spring to support new growth, followed by an accumulation of sugars and proteins in the leaf canopy with increased photosynthetic capacity during the growing season. With the onset of autumn senescence, soluble sugars from aboveground organs are converted to stored starches in the roots and rhizomes (Zasada *et al*., 1994; Landhausser and Lieffers, 1997, 2002). Because aboveground recruitment in clonal species depends on nutrient reserves in belowground structures, this cycle of nutrient shunting is important to the maintenance of the stand, and a linear quantitative relationship between root stores and new shoots or suckers has been shown in multiple species (Zasada *et al*., 1994, Landhausser and Lieffers, 1997, 2002).

Carbohydrate and nutrient dynamics in Arundinarieae seem to follow along the same lines as those of other woody clonal species (Li *et al*., 1998a). Although the evergreen nature of bamboo reduces the need to support the large spring leaf flush seen in deciduous species, rapid shoot production and elongation of multiple ramets within a few weeks' time places the same demands on nutrient stores. Because the season of active

shoot growth corresponds with a time when senescence occurs in the oldest leaves, photosynthetic capacity is reduced and new clones must rely even more on stored nutrients for growth (Li *et al*., 1998a). Apart from seasonal nutrient cycling, Li *et al*. (1998a) also found that 1st-year leaves of *Phyllostachys pubescens* had a greater photosynthetic capacity and contained more TNC and other nutrients than 2nd-year leaves. Because many bamboos experience a multi-annual cycle in leaf shedding, leaf density, and average leaf maturity (Li *et al*., 1998a, b), nutritional quality of an entire leaf canopy could vary from year to year as well. Leaves overall contain much more TNC, N, P, and K than the woody stem or culm, but the culm has a significant role in nutrient storage, with 38% of total stored TNC in *P. pubescens* located there, as opposed to 26% in the rhizome (Li *et al*., 1998a).

Despite the extensive body of work on clonal nutrient dynamics with respect to plant physiology and life history, few studies (Greenway, 1999; Tabet *et al*., 2004) examine nutrient composition of bamboo as a forage. One key primary consumer is the giant panda (*Ailuropoda melanoleuca* David; Chorn and Hoffman, 1978), a specialist herbivore whose diet consists almost exclusively of Arundinarieae (99% or more of the diet; Schaller *et al*., 1985; Edwards *et al*., 2006). Despite numerous adaptations of the skeletal structure for processing such a foodstuff (e.g., broad, large molars, thickened tooth enamel, enlarged muscular attachments on the skull, and the modified radial sesamoid or "pseudothumb"), the giant panda possesses no adaptations of the digestive tract to assist with fiber digestion (Schaller *et al*., 1985; Edwards *et al*., 2006). Consequently, its digestive efficiency is among the least of all land mammals (10 to 40% on a bamboo-only diet; Schaller *et al*., 1985; Long *et al*., 2004; Edwards *et al*., 2006;

Sims *et al*., 2007), and maximizing nutritional quality of forage becomes crucial to survival and reproduction of this critically endangered species.

One key strategy employed by giant pandas to optimize nutrient intake is extreme dietary selection: foraging pandas, both in the wild and in captivity, make deliberate choices about which pieces of bamboo they will consume, using smell and taste to identify plants that are presumably greater in nutritional value. This selection applies to bamboo species, plant parts consumed, and individual ramets within a species (Schaller *et al*., 1985; Tarou *et al*., 2005; MZS, 2006). However, this selection varies seasonally, again both in the wild and in captivity, particularly with regard to plant-part consumption. During late spring, summer, and autumn, giant pandas consume primarily bamboo leaves; during winter, they shift to a diet composed mainly of culm material. During springtime bamboo-shoot emergence, shoots are consumed preferentially when available, and immediately after this period, animals shift once more to leaf consumption (Schaller *et al*., 1985; MZS, 2006). In the wild, these shifts in plant-part selection co-occur with seasonal migrations in altitude, and therefore with changes in bamboo species availability (Schaller *et al*., 1985; Reid and Hu, 1991). In captivity, plant-part shifts can occur when consuming the same species of bamboo year-round (MZS, 2006).

The underlying cause of such seasonal diet shifts is unknown, but presumably the animals respond to either changes in bamboo or circannual rhythms within pandas themselves. We sought to investigate the former by following within-year bamboo nutritional composition, with respect to both season and stage of ramet maturity. To further examine any long-term factors that may affect bamboo composition and therefore

nutritional quality or palatability, we incorporated 2 additional independent variables into our investigation: year-to-year ramet age and aboveground disturbance.

Ramet maturity and aging may substantially affect bamboo composition and palatability, particularly with regard to fiber composition and biogenic silica. Cell walls and fiber cells in bamboo culm experience substantial thickening and lignification during the first year of growth (Liese and Weiner, 1997; Murphy and Alvin, 1997). Both of these processes also continue at a slower rate in successive years, with progressive culm lignification through at least year 3 (Murphy and Alvin, 1997). Progressive lignification of bamboos results in an increase in the indigestible portion of their makeup. Wang *et al*. (2007) and Schaller *et al*. (1985) often saw "topping" of bamboo ramets by wild pandas, leaving behind stumps that vary in height depending on season (higher in winter than summer) and age (stumps from older ramets were taller). Because lignification of bamboo culms begins at the base (Murphy and Alvin, 1997), such patterns in vegetation clipping could indicate selection based on fiber characteristics. In most plants, increases in total fiber and lignification with season or maturity also correlate with decreases in essential nutrients such as crude protein and available energy (Robbins, 1993; Kramberger and Klemencic, 2003), thereby reinforcing cues for negative selection by herbivores. Thus, in general, herbivores consistently select against plants or plant portions with increased fiber (Robbins, 1993). For giant pandas in particular, which lack the ability to break down all but the most digestible fiber fractions, selection against very fibrous plant tissues would seem to have particular importance.

The giant panda does face direct threats to survival in the form of poaching or by-catch in snares set for other species (Schaller *et al*., 1985). But like many other

endangered and threatened species, a greater problem is the pervasive influence of habitat disturbance. The historic range of the species, which once included much of China, has been progressively reduced to smaller areas at higher elevations as bamboo forests have been turned into agricultural lands. The government of China has made significant strides to control human settlement in wildlife reserves and to reduce the rate of deforestation, however clearing of land for crops or logging of the forest for firewood or raw materials does still occur (WWF, 2004). Schaller *et al*. (1985) documented significant and large-scale changes to bamboo life-cycle events as a result of logging. It follows that such disturbances also may impact the biochemical composition of bamboo. The most immediate and frequently reported effect of plant disturbance that is relevant to herbivores is an increase in plant chemical defenses. Fortunately, our data (unpublished) indicate that allelopathy in temperate bamboos is likely minimal. However, important physiological changes may still occur in disturbed bamboo, and potentially alter its nutritional composition and quality.

Changes in clonal biochemistry in response to disturbance are complex, though the one constant in all systems is a major alteration in nutrient cycling and source-sink dynamics following aboveground perturbations. Tschaplinski and Blake (1995) found that removal of clonal shoots from *Populus* spp. dramatically altered carbon metabolism, causing mobilization of free sugars and depletion of starch stores, which in turn stimulated photosynthesis in remaining tissues. This photosynthetic demand altered the structure and physiology of the clone: in pruned trees, leaf production was greater and gas exchange in leaves much faster than in unpruned trees. Enhanced photosynthetic capacity resulted in increased production of new assimilates, which were then transported

to the root system at a much faster rate in pruned trees (Tschaplinski and Blake, 1995), presumably to replenish root stores.

Bamboos seem to respond in a similar fashion. Harvested tropical bamboo stands in northern India showed greater translocation of nutrients below ground (Tripathi and Singh, 1994). Aboveground disturbance in temperate bamboos can likewise change normal cycles of leaf density, photosynthetic capacity, and in turn recruitment (Li *et al*., 1998a,b). In mature stands that are balanced with respect to new vs. old leaves, and therefore do not undergo annual oscillations in average leaf maturity (Li *et al*., 1998b), catastrophic disturbance could catalyze large cyclical variances in new leaf production, photosynthetic capacity, and new shoot recruitment (Kleinhenz and Midmore, 2001). A great deal of the literature focuses on stored nutrient depletion in the belowground compartments after disturbance (Zasada *et al*., 1994; Tschaplinski and Blake, 1995; Reichenbacker *et al*., 1996; Landhausser and Lieffers, 1997, 2002; Li *et al*., 1998a,b), but depletions in culm stores of remaining vegetation could also occur (assuming physiological integration), affecting palatability and nutritional quality of culm tissues following severe aboveground alterations.

Little to no information exists on the effect of harvest on the biochemistry of bamboos in temperate regions, particularly with regard to giant panda herbivory. However, Reid and Hu (1991) and Wang *et al.* (2007) observed that wild pandas avoid previously foraged sites. This behavior could simply result from a decrease in available biomass following disturbance (Wang *et al*., 2007). On the other hand, it could indicate alterations in any of the variables mentioned previously (fiber characteristics, silicification, carbohydrate or nutrient dynamics) and resulting cues for negative dietary

selection. The present study originated in part after anecdotal reports that a pair of captive pandas began to avoid bamboo cut from the same stand(s) after a number of years [J. Tang, Ocean Park Hong Kong, personal communication]. We posited that existing fertility regimes may not have kept up with soil nutrient depletion, or may have introduced compounds that reduced palatability [B. Baldwin, personal communication] – or possibly that 1) progressive ageing of the bamboo stand resulted in diminished nutritional quality and palatability over time, or 2) aboveground disturbance in the form of harvest pressure may alter the biochemistry of the remaining ramets, leaving them unpalatable to these specialist herbivores.

Procurement of bamboo represents the greatest cost for institutions housing giant pandas (MZS, 2006). Mismanagement of a bamboo stand over the long term could result in reduced palatability, wasted bamboo, and wasted money and effort. Captive animal managers must find a way to propagate, manage, and harvest bamboo in such a manner that quantity, quality, and diversity are all optimized. Meanwhile, the greatest single concern for wild panda conservation in China is management of native habitat (WWF, 2004). Land clearing in or near wild panda reserves, even on a small scale, could affect surrounding habitat. Thus, information on the complexities of bamboo biochemistry is important not only to captive animal institutions, but also to managers of wild panda habitat, faced with a difficult balance between the needs of animal and human populations. Proper understanding of factors that affect bamboo composition and physiology, as well as the manner in which pandas respond to intrinsic changes in bamboo, is essential. The present study sought to quantify the effects of season, within-year bamboo maturity, year-to-year bamboo age, and aboveground disturbance intensity

on the nutritional composition of bamboo. We also sought to extend previous investigations on seasonal composition of bamboo (Tabet *et al*., 2004), by collecting multi-year data.

Material and methods

Research site

We conducted a 2-year investigation (June 2005 to June 2007). The study was conducted entirely within a 4-ha plot of land (35° 7'57"N, 89°49'49"W) at the Shelby County AgriCenter in Memphis, Tennessee, USA (Figure 2.1), operated by the Memphis Zoo (MZ) for the purpose of growing bamboo to feed giant pandas. The site was established in 2001 on a former cotton field, and originally planted with 7 bamboo species. Commercially-cultivated bamboo was bought from local nurseries and planted in 2001 and 2002, in clumps of 2 to 5 ramets, spaced 0.5 to 1 m apart, to establish 0.4-ha monoculture plots maintained in 10 rows per plot. At the initiation of the study, aisles between rows had historically been maintained by MZ personnel, by periodic mowing and use of glyphosate herbicide. After initiation of the study, mowing within experimental enclosures was suspended. This location is characterized by sandy loam soils, bordered by manmade ponds to the west and south, a 2-lane local-access road to the north, and agricultural fields (historically cotton) to the east and just across the northern road.

Study species

The bamboo species selected for this study all belong to genus *Phyllostachys*, one of the largest and most widespread genera of woody bamboos (Renvoize and Hodkinson,

1997). Bamboos of this genus are easily cultivated, commercially available, and grow well in many locations all over the world. For that reason, many zoos that house captive pandas rely on *Phyllostachys* spp. as their bamboo staple (Edwards *et al*., 2006). The 3 focal species of this study (*Phyllostachys aureosulcata,* PLLAU; *P. glauca,* PLLGL; and *P. rubromarginata*, PLLRU) are among those preferred by the Memphis pandas (constituting 66% of their annual diet; MZS, 2006), and are commonly fed by other zoos as well (Edwards *et al*., 2006, Sims *et al*., 2006). *Phyllostachys* spp. are monopodial bamboos, with leptomorphic ("running") rhizome systems (Kleinhenz and Midmore, 2001). Primary shoot production occurs in spring (April through May at this location), with an occasional secondary shoot crop in autumn (August through September), depending on local conditions in a given year.

Experimental design

Within each of the 3 species plots under study, we established 4 replicated enclosures (approximately 24 x 15 m each), such that equal bamboo density within enclosures was optimized. A sampling grid was established, and each enclosure was divided into 3 6 x 9-m subplots with a 3-m buffer around the edge of the enclosure, within which each of 3 experimental disturbance treatments were assigned to subplots randomly: control (no bamboo removal), 3%/year removal of individual live ramets, and 20%/year removal (Figure 2.2). Disturbance intensities were selected to simulate typical grazing rates by wild giant pandas (3% removal; Wang *et al*., 2007) and harvest rates typically employed by zoos feeding giant pandas (20%; MZS, 2006).

At study initiation, at least 50 live ramets per subplot were randomly pre-identified for later nutritional sampling (located evenly throughout each subplot), and

tagged to prevent removal during application of disturbance treatments. Ramet removal for treatment effects occurred at quarterly intervals (January, April, July, October), with live ramets removed in a uniform manner throughout the stand. Every autumn (September or October), live ramet densities were quantified at four locations within each subplot, and used to estimate total live ramet density per subplot, from which biomass removal rates were calculated for the subsequent 4 quarters. A fertility regime was applied in a split application at the initiation of the study (7 June 2005), and each autumn (November) and winter (January or February), at least 1 month prior to subsequent bamboo sampling. Soil was sampled in October from 2 locations per replicate enclosure, pooled by bamboo species, and fertilizer was applied in quantities recommended for temperate forage grasses by the Mississippi State University Cooperative Extension Service (MCES) Soil Testing Laboratory.

Sample collection

Sampling of bamboo for nutritional analysis was intended to occur at 9 times per year for each bamboo species, at points throughout the year corresponding to significant developmental stages of bamboo growth and maturation: 1 = early shoot emergence (ramet 15 to 45 cm tall); 2 = later shoot emergence (ramet ~1 m tall); 3 = ramet elongation (maximum height has been reached, sheaths are shed, branches jointed); 4 = leaf emergence; 5 = 30 days after leaf emergence; 6 = 90 days after leaf emergence; 7 = first freeze (mid-November); 8 = mid-winter (January); 9 = preparation for shoot emergence (March). Once sampling began, it became evident that stages 3 and 4 were difficult to distinguish, and so stage 4 sampling was eliminated, leaving 8 sampling points per year. All sampling occurred within 2 m of the eastern edge of historic mowed

aisles, to control for variation in peak sun angle. In Year 1, 1 ramet per treatment per enclosure was cut at the base (point of contact with the soil, or just above the point of lateral rhizome branching), and removed for processing (12 samples per developmental stage per species). For stages 1 and 2, an additional 3 and 1 ramets (respectively) were removed and pooled by subplot, to provide adequate sample mass for analyses. As each year's shoot crop reached stage 6 (August to September), at least 40 ramets < 1 year old were located within 0.5 m of previously-tagged ramets, and themselves tagged with a different color, to allow for comparisons among age classes in subsequent years. Thus, in Year 2, at each sampling point, 1 ramet > 1 year old and a paired ramet < 1 year old was sampled (24 total samples per developmental stage per bamboo species), and in Year 3, 1 ramet > 2 years old, 1 ramet > 1 year old, and 1 ramet < 1 year old were sampled (36 samples per stage per bamboo species). Location of sampled ramets was recorded with respect to the sampling grid.

As sampling proceeded, all cut ramets were kept in shade to prevent sun exposure, and bundled into plastic sheaths within 1 hour of sampling. Bundles were placed in the back of a pickup truck, covered with ice, and topped with a sheet of polystyrene home insulation. If sampling lasted an entire day, several applications of ice were performed as samples were added to the truck bed, such that no sample went longer than 2 to 3 hours before cooling. Samples were transported to Mississippi State University (MSU) North Farm Complex, and placed in a 5 °C walk-in cooler. During sample processing, ramets were removed individually from the cooler and replaced after processing, such that no sample was outside of refrigeration longer than 1 hour after arrival at MSU. Ramets from stages 5 through 9 were hosed to remove surface

contaminants (dirt, bird feces, etc.) and separated into leaf, branch, and culm (Figure 2.3). Leaf and culm samples were dried to constant mass at 60 °C, and ground in a Wiley Mill to pass through a 2-mm screen. Stages 1 through 3 were dried and ground entirely. Giant pandas consume only leaves and culm, so all branch samples were banked, as well as samples from stages 6 and 8. Shoot, leaf, and culm samples from stages 1, 2, 3, 5, 7, and 9 were quantitatively analyzed for nutritional composition.

Analyses

Nutritional analyses were performed at the H. W. Essig Nutrition Laboratory, MSU. Crude protein (CP; Kjeldahl N; FOSS North America, Eden Prairie, Minnesota), ash, lipid (crude fat via ether extract), and neutral- and acid-detergent fiber (NDF and ADF; ANKOM Technology Corporation, Fairport, New York) were quantified via official methods (Van Soest *et al*., 1991; AOAC, 2000). Analysis of mineral composition (P, K, Ca, Mg, S, Fe, Mn, Zn, Cu, B) was performed via inductively-coupled argon plasma with flame spectroscopy by the MCES Plant Analysis Laboratory.

Statistical comparisons of nutritional compounds were performed via Analysis of Variance. Because of substantial differences in origin of ramets and planting history among PLLAU, PLLGL, and PLLRU, bamboo species were analyzed separately. Significant compositional differences among shoot, leaf and culm tissues are well established (Dierenfeld *et al*., 1982; Li *et al*., 1998a,b; Tabet *et al*., 2004; Edwards *et al*., 2006; MZS, 2006; Sims *et al*., 2007), and all analyses were separated by plant part as well. For this study, we defined 3 distinct seasons based on significant events in bamboo life-history and seasonal weather patterns, which also coincide with seasonal changes in giant panda diet preference (MZS 2006): Spring (preparation for shoot production) =

February through May, Summer (peak biomass and photosynthesis) = June through September, and Winter (senescence) = October through January.

Analyses of effects through time (main effect of sampling date) were performed via mixed-model repeated-measures ANOVA (PROC MIXED; SAS Institute, 2012) , with subplot as the repeated unit, sampling date as the main (random) effect, and ramet age as an additional term in the model. Effective degrees of freedom were determined using Satterthwaite approximation.

Analyses of main effects of ramet maturity (for ramets < 1 yr old) and ramet age (for ramets ≥ 1 yr old) were performed via repeated-measures ANOVA in a general linear model (PROC GLM; SAS Institute, 2012), with subplot as the repeated unit. For analysis of maturity, study year was an additional term in the model;for analysis of age, season was an additional term. To determine effects of aboveground disturbance, a repeated-measures split-plot ANOVA was performed (PROC MIXED), with replicate enclosure as the repeated unit, sampling date as the main-plot factor, and disturbance treatment as the subplot factor.

Monthly weather parameters for the study site were obtained from the U.S. National Oceanic and Atmospheric Administration (NOAA), taken at an observation post located at the Shelby County AgriCenter (35° 7'47"N, 89°48'13"W), 2.5 km from our study site (Table 2.1, Figure 2.4). To test for potential covariates, we performed correlations (PROC CORR; SAS Institute 2012) between response variables and 1) mean monthly temperature, and 2) total monthly precipitation. For variables with significant correlations, we then tested for homogeneity of the slope of the covariate relationship

(PROC GLM, with sampling date as a random effect), before performing Analyses of Covariance. For all analyses described herein, a significance level of $\alpha \leq 0.05$ was used.

Results

Temporal effects

Mineral analysis was not available for the entire the duration of this study, nor was proximate or fiber analysis for the latter portion of culm samples. Thus, analyses of culm minerals were not performed after November 2005, and remaining analyses of culm samples were not performed after July 2006. Likewise, nutritional analyses of PLLGL and PLLRU shoots were not performed in Year 2 of the study. For all other samples and analyses, data are presented for samples taken between July 2005 and June 2007.

After accounting for effects of ramet age, differences by sampling date were found in all nutrients, plant parts, and species analyzed ($P < 0.001$; Tables 2.2, 2.3, 2.4; Figures 2.5, 2.6, 2.7). For CP, lipid, P, Mg, S, Fe, Mn,, and Zn, we observed a general linear increase in concentration over the length of the study, particularly in leaves, such that these nutrients were at their greatest concentration at the end of Year 2. Ash concentration in PLLGL (Table 2.3, Figure 2.6) and PLLRU (Table 2.4, Figure 2.7) rose progressively within a given year, reached its peak each March, and then decreased to its least concentration in May. Ca followed a similar trend, reaching peak concentration between April and June, and falling immediately thereafter, though for both PLLGL and PLLRU, Ca concentration in November 2006 was greater than at surrounding sampling dates (Figures 2.6, 2.7). Leaf K reached peak concentrations in May through July for all bamboo species, and lowest concentrations in March. For all 3 species, Cu increased from study initiation to July 2006, fell, and began increasing again.

Ramet maturity and age

Evaluating ramets less than one year old, within-year mean nutrient content differed ($P < 0.01$; Table 2.5, 2.6, 2.7; Figures 2.8, 2.9, 2.10) by stage of development for all nutrients and bamboo species except S and B in PLLGL (Table 2.6, Figure 2.9). For PLLAU, older shoots had greater concentrations of NDF and ADF; concentrations of CP, lipid, and all minerals but Mn were greater in the youngest shoots, and decreased as shoots lengthened (Table 2.5). The same was generally true in PLLGL and PLLRU, however no differences were evident between older and younger shoots in NDF, lipid, K, Ca, Mg, S, Mn, or B for PLLGL (Table 2.6), nor in ash, ADF, lipid, K, Ca, Mg, Fe, Mn, or B for PLLRU (Table 2.7).

As leaves matured in PLLAU, greater conentrations of CP, ash, Ca and Mn and less K were observed (Table 2.5, Figure 2.8). PLLGL leaves showed progressively greater ash, P, Fe, Mn, and less K (Table 2.6, Figure 2.9), and PLLRU leaves became more concentrated in ash, Ca, S, Mn, and Zn as they matured, with less K, and Cu (Table 2.7, Figure 2.10). Maturing PLLAU culm material had greater concentrations of CP and P and less K (Table 2.5, Figure 2.8). PLLGL culm contained more Fe and less ash in more mature tissues (Table 2.6, Figure 2.9), and PLLRU culm lost ash concentration as it matured (Table 2.7, Figure 2.10).

For ramets one year old or greater, after accounting for seasonal effects, differences in least square mean nutrient concentration between 1- and 2-year-old ramets were detected ($P \leq 0.05$) for some but not all nutrients and species analyzed (Table 2.8). Two-year-old ramets contained greater concentrations of CP (PLLAU), lipid (PLLAU, PLLGL), and NDF (PLLGL, PLLRU), and less ADF (PLLAU) and ash (PLLGL). In

general, older ramets also showed greater P (PLLAU, PLLGL), K (PLLAU, PLLGL), S (PLLRU), and Cu (PLLGL, PLLRU). Younger ramets had greater concentrations of Ca (PLLGL, PLLRU), Mg (PLLRU), Fe (PLLGL, PLLRU), Zn (PLLRU), and B (PLLRU). For Mn, differences were reversed between PLLAU and PLLGL: for the former species, older ramets showed greater concentrations; for the latter, ramets lost Mn with age (Table 2.8).

Disturbance

Split-plot repeated-measures analyses detected no effects of disturbance treatment ($P > 0.33$), with one exception. For PLLGL, greater concentrations of NDF were detected in ramets from 3%-annual-removal subplots than from 20% annual removal, with control ramets intermediate ($F_{2,156} = 5.41$, $P = 0.005$; Table 2.9).

Weather

Nutrient concentration correlated ($P < 0.05$) with both mean monthly temperature and total monthly precipitation for protein, ash, ADF, Ca, S, Fe, Mn, and Zn. NDF, lipid, and P only correlated with mean monthly temperature ($P < 0.05$), and K, Mg, and Cu only correlated with total monthly precipitation ($P < 0.05$). Of those variables, the assumption of homogeneity of the slope of the covariate relationship was met in only 5 cases; results of subsequent ANCOVAs are presented in Tables 2.10 and 2.11.

Soil chemistry

Results of soil samples taken at the initiation of the study and thereafter every October are presented in Table 2.12. For all bamboo stands, pH decreased over the length of the study, P, Mg, Zn, and Na increased, and Ca decreased but rebounded in

2007 for PLLAU and PLLRU. Between 2006 and 2007 in particular, cation-exchange capacity (CEC) increased for all bamboo species. Between-year differences were greater between 2006 and 2007 than between 2005 and 2006 for P and K.

Discussion

Temporal effects

During winter 2006 to 2007, Shelby County experienced a stochastic peak in the local population of red-winged blackbirds (*Agelaius phoeniceus*). Because of this species' tendency to form large communal flocks in the winter, and the attraction of the MZ bamboo stands as a sheltered roosting location among agricultural fields, thousands of birds descended upon our study site each night between November and February. The resulting deposition of guano was impressive, covering the soil surface between bamboo rows with 2 to 5 cm of organic matter by late January, and coating most ramets with notable concretions of urates.

This phenomenon very likely resulted in changes in soil chemistry that in turn drove bamboo biochemistry over time (Tables 2.2, 2.3, 2.4; Figures 2.5, 2.6, 2.7). Particularly in spring 2007, we observed significant increases in CP, lipids, P, Mn, and Zn in shoots and leaves, and in Cu in shoots. Compared to the prior spring, bamboo leaves in spring 2007 had more K, S, and Fe, and less Ca and ADF. Although soil testing only occurred only in autumn, even in October 2007 we found significantly altered soil chemistry compared to the prior year (Table 2.12), again likely driven by guano deposition. We presume that our observed decrease in leaf ADF in spring 2007 may be attributed to increases in so many other nutrients, and simple principles of proportion. A portion of the progressive increase in plant tissue proteins could potentially be attributed

to the fertility regime, but after the initial application in spring 2005, no other nutrients aside from NH_4NO_3 were applied – meaning that the increases in tissue phosphorus and potassium from 2006 to 2007 were not anthropogenic. Likewise, we observed a depression in soil pH from 2006 to 2007, despite the aggressive application of lime during that period of time.

Garcia *et al*. (2002) and Breuning-Madsen *et al*. (2010), reported similar findings in soil chemistry and vegetation near seabird roosting sites, with significant increases in soil C, N, P, K, and Ca in the latter study, and increases in soluble soil K, Mg, Ca, and NO3, and in available P, K, Fe, and Zn in the former. Garcia *et al*. (2002) tested nutrient composition of vegetation near the roosting sites, and likewise found significant increases in leaf concentrations of N, P, K, and Zn, and decreases in leaf Ca. Both studies reported significantly lower pH near seabird roosts, compared to control sites.

Aside from changes in plant nutrients associated with bird colonization, we also observed what seemed to be normal annual cycles in a handful of nutrients. For PLLGL and PLLRU, leaf ash increased from the time of leaf emergence (summer) until just before shoot production (late spring), and then dropped once more (Tables 2.3, 2.4; Figures 2.6, 2.7). A majority of total ash in bamboo is made up of biogenic silica (Greenway, 1999), and others have observed a similar increase in silica content of leaves during winter months (Schaller *et al*., 1985). It is possible we were observing a similar phenomenon, or simply a change in proportion of leaf nutrients during winter downregulation of photosynthetic enzymes (Kleinhenz and Midmore, 2001). Leaf K decreased from summer through winter, increasing again in spring and early summer (Tables 2.2, 2.3, 2.4; Figures 2.5, 2.6, 2.7) – again potentially associated with peak

photosynthesis in early summer (Kleinhenz and Midmore, 2001). Again for PLLGL and PLLRU, leaf Ca reached its peak in March of each year, followed by a decline to its minimum concentration in July (Tables 2.3, 2.4; Figure 2.6, 2.7). Tabet *et al.* (2004) also saw a springtime peak in Ca concentration in *P. aureosulcata* leaves, followed by a reduction in early summer, although they did not observe similar patterns to ours in concentration of this nutrient during the rest of the year, nor did they present data across multiple years.

We also observed changes in year-to-year weather trends over the course of this study. In summer 2006, the study site received less rainfall than the previous year, especially during the period of peak temperatures (Table 2.1, Figure 2.4). In spring 2007, seasonal severe weather and accompanying rainfall was less than usual. Although we noted subsequent changes in bamboo biomass production, recruitment, and mortality at the study site (unpublished data), the interactions between weather and bamboo composition proved too complex to fully investigate. For those variables that we were able to analyze via ANCOVA, adjusted means were similar to those unadjusted for weather variables (Table 2.11), indicating that weather patterns did not account for the changes over time already discussed.

Ramet maturity and age

Bamboo ramets, particularly those of monopodial species, undergo a distinct progression in nutrient accumulation and availability from shoot emergence to ramet maturity. Rapid shoot elongation is achieved through a preparatory period of significant cell proliferation in rhizome buds, followed by swift expansion of internodes via influx of water into the cytosol (Kleinhenz and Midmore, 2001). As shoots elongate, parenchyal

fiber development begins, and fiber maturation occurs in earnest between full elongation and ramet maturity; by the time ramets reach 1 year of age, culm fiber content is at its maximum (Murphy and Alvin, 1997; Kleinhenz and Midmore, 2001). As new leaves emerge, they reach their highest photosynthetic capacity at full expansion, followed by a progressive decrease in photosynthesis, particularly into autumn and winter as falling temperatures limit enzymatic efficiency (Kleinhenz and Midmore, 2001).

Particularly with respect to shoot nutrient concentration, our findings reflect these patterns of growth and develoment. The youngest shoots had the greatest concentrations of soluble nutrients and minerals, and with the beginnings of lignification by Stage 3 of development (full elongation), ADF and NDF increased substantially, with a resulting proportional decrease in non-structural components. As expected, we observed a linear decrease in leaf K with maturity, although we also expected to see a decrease in CP and P as in Zhou and Wu (1997) and Nickley (2001). This was true for PLLAU (greater CP in mature leaves) and PLLGL (greater P), but not for PLLRU. Nickley (2001) did see increases in ash between 6-month-old and 12-month-old leaves, similar to observations in this study. Again, increases in ash concentration could indicate winter silicification of leaf tissues. Our analyses of nutrient concentration by growth stage were adjusted for year of study, thus unexpected increases in leaf nutrient concentrations (Fe, Ca, Mn, Zn) could not be explained by blackbird guano deposition discussed previously.

A great deal of the literature on ageing of bamboo, particularly with respect to timber production, focuses on fiber characteristics. Prior investigations found cell wall thickening (Liese and Weiner, 1997) and progressive lignification of culm structures (Liese and Weiner, 1997; Li, 2004) after 1 year of age. Li (2004) also found increases in

holocellulose and α-cellulose. We did not have sufficient 2-year-old culm samples to truly investigate this question, but we did see a small increase in NDF between 1-year-old and 2-year-old ramets for PLLGL and PLLRU, potentially reflecting such changes in fiber characteristics.

With regard to leaves, it is important to note that in monopodial bamboos, leaf life span is no longer than 2 years old, and leaves of 1-year-old ramets in particular are shed before subsequent shoot emergence (Li et al., 1998a,b; Kleinhenz and Midmore, 2001). Thus, increases between 1-year-old and 2-year-old ramets in nutrients such as CP, P, K, S, and Cu could very well reflect leaf turnover and return to peak photosynthetic activity. Embaye *et al*. (2005) likewise found increases in leaf percent N with ramet age in an African species of monopodial bamboo, but also found decreases in percent P and K, and an increase in percent Ca, converse to our findings. However the study also compared ramets across greater time scales, estimating ramet age in a natural forest and classifying them into ranges of < 1 yr, 1 to 3 yr, and > 3 yr. Given these constraints, it was not possible for the authors to investigate the nuances of biennial leaf turnover.

Disturbance

Aboveground disturbance appeared to have little effect on bamboo nutritional composition in this study. Although we detected statistical significance for NDF in PLLGL, the differences in values across disturbance treatments were probably not biologically significant; for all other nutrients, no disturbance differences were detected. One potential explanation is resiliency in the face of such disturbance. We have found evidence that disturbance affects bamboo life-history traits and biomass production (unpublished data), however those effects may not have resulted in compositional

differences. Perhaps the rates of biomass removal in this study were not great enough to induce biochemical changes in remaining vegetation, and a greater amount of disturbance would be necessary before significant changes in clonal nutrient dynamics occurred. The timing of disturbance also matters a great deal in clonal species: if ramets are removed during the belowground storage period, nutrient loss to the clone is not significant, and growth and composition of resulting new ramets is not affected. If, on the other hand, aboveground biomass is removed during peak photosynthesis, the ability of the clone to muster sufficient nutrients to support normal physiological function is compromised (Tripathi and Singh, 1994; Li *et al*., 1998a,b; Shanmughavel and Francis, 1996, 2001). Our disturbance treatments were spread out across an entire year; if treatment application had been concentrated during a particular period of time, other effects may have been observed.

Many clonal species are able to mitigate the effects of disturbance or mount a defensive response by taking advantage of physiological integration and sharing of resources among ramets (Herms and Mattson, 1992; Gough *et al.* 2002; Peltzer, 2002; Wilsey, 2002). However, evidence for clonal integration in bamboos is equivocal. Ramets of dwarf bamboo (*Sasa* spp.) do appear to communicate, enabling support of ramets in resource-poor patches by those in resource-rich areas (Saitoh *et al*., 2002). Wang *et al*. (2007), on the other hand, failed to detect any evidence of clonal dynamics in structural response to herbivory. They suggested that ramets were acting as individuals, with hormonally mediated compartmentalization of stressed portions of the clone (Haukioja, 1991). The ability of clonal plants to regulate and vary the degree of

physiological integration among ramets complicates attempts to characterize disturbance effects.

Although the subplots from which we harvested bamboo were randomized in location, it was potentially possible for 3%- and 20%-removal subplots to be physically close together. Dye techniques have been used to identify closely-spaced sister ramets, however a method does not yet exist to identify members of an entire clone [W. Wang and S. B. Franklin, University of Memphis, personal communication] – particularly in rhizomatous rather than tillering bamboo species, where sister ramets can be physically distant. Thus, it is very possible that portions of clones in our study straddled subplots. If no physiological integration occurred in these clones, as in Wang *et al*. (2007), then our subplots were truly independent. However, if this were the case, we would also expect remaining ramets to behave as if no disturbance occurred. If, on the other hand, integration were occurring, disturbance effects may have been mitigated or spread over a larger area, confounding our results. The only true way to parse these two possibilities would be to plant a bamboo stand such that clones do not overlap, or to identify members of a clone and space treatments out sufficiently that two treatments did not affect a single clone. As we were working in a relatively small (0.4-ha), already-established stand, neither experimental design was possible.

Finally, there may indeed have been biochemical changes to aboveground disturbance, but not in the nutrients we analyzed. A great deal of the literature on responses of clonal species to clipping or herbivory focuses on disruptions to annual cycles of carbohydrate flux (Zasada *et al*., 1994; Tschaplinski and Blake, 1995; Reichenbacker *et al*., 1996; Landhausser and Lieffers, 1997, 2002; Li *et al*., 1998a,b;

Price and Marshall, 1999; Kleinhenz and Midmore, 2001; Klimes and Klimesova 2002). Because giant pandas are unable to utilize most dietary fiber like other herbivores, non-structural carbohydrates must represent a significant source of energy for this species (Schaller *et al*., 1985; Edwards *et al*., 2006). Given the scale of the current study and the time delay between clipping of ramets and transport to the laboratory, a proper examination of soluble sugars, a major component of TNC, would not have been possible. Starches, on the other hand, are much more stable compounds, and whereas starch analysis was not part of the scope of this study, we recommend close examination of this nutrient in future investigations. Prior evidence (Liese and Weiner, 1997; Kleinhenz and Midmore, 2001) also indicates that starch and sugar accumulation in culm tissues appears to change with ramet age, and may be related to seasonal giant panda diet selection (Bissell *et al*., 2006), as culm accumulations of TNC can be substantial (Kleinhenz and Midmore, 2001).

In addition to the giant panda, a number of other threatened or endangered species depend on bamboo as a primary food source, or as a significant component of the diet. These include the red panda (*Ailurus fulgens*; Bleijenberg and Nijboer, 1989), bamboo lemurs (*Hapalemur* spp.; Tan, 1999), and the mountain gorilla (*Gorilla beringei*; Rothman *et al*., 2007). All of these species also face some degree of habitat loss or modification. The key to conservation is habitat restoration (WWF, 2004): expanding existing refuges, and establishing protected corridors to allow gene flow among isolated metapopulations (Hunter *et al*., 2003). However, to do so without consideration for the nutritional environment is to set these animals up for failure.

Factors such as year-to-year clonal growth dynamics, seasonal nutrient flux, and potential effects of disturbance – especially with regard to scale and timing of biomass removal – have direct impact on the availability and nutritional quality of forage in a natural bamboo forest. To better understand panda ecology and conservation, we urge field researchers to more closely examine nutrient dynamics of bamboo in these animals' native habitat. Availability of easily-digestible energy sources such as non-structural carbohydrate may be particularly important and especially variable, and could have significant bearing on survival and fitness of individuals and populations. These nutrients have been seldom examined in cultivated bamboo and (to our knowledge) never studied *in situ*, and merit much deeper scrutiny.

Table 2.1 Weather data for study period.

Year	Month	Total precipitation (cm)	Mean temperature (°C)
2005	May	0.78	19.9
	Jun	2.29	25.5
	Jul	5.99	27.2
	Aug	4.05	28.4
	Sep	1.37	24.7
	Oct	0.43	16.2
	Nov	2.08	11.9
	Dec	1.54	3.9
2006	Jan	5.08	8.3
	Feb	2.75	3.8
	Mar	2.36	11.4
	Apr	3.02	19.4
	May	2.85	21.3
	Jun	1.90	25.2
	Jul	0.37	27.9
	Aug	2.25	28.8
	Sep	2.00	21.9
	Oct	1.81	15.9
	Nov	1.91	10.4
	Dec	4.40	8.0
2007	Jan	3.13	5.3
	Feb	1.60	4.3
	Mar	0.41	16.3
	Apr	2.66	14.8
	May	0.69	22.9
	Jun	1.50	26.6
	Jul	2.87	26.8
	Aug	0.56	30.4
	Sep	1.28	24.60
	Oct	3.27	18.90
	Nov	2.65	11.30
	Dec	3.00	7.90
2008	Jan	3.15	3.90
	Feb	1.93	6.50
	Mar	5.66	10.80
	Apr	7.07	15.20
	May	5.05	20.90
	Jun	1.64	26.70
	Jul	0.98	27.70
	Aug	2.74	26.00

Note: All data were taken from a NOAA weather station located at Shelby County AgriCenter, Memphis, Tennessee, USA (35° 7'47"N, 89°48'13"W), 2.5 km from the study site.

Table 2.2 Nutrient concentration of bamboo by sampling date and plant part: *Phyllostachys aureosulcata.*

	Percent (dry-matter basis)[1]									
	CP[2]		Ash		NDF[3]		ADF[4]		Lipid	
Sampling date	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N
Shoots										
28-Apr-06, 15 to 45-cm shoots	25.03[a]	12	8.90[a]	12	59.68[a]	12	24.56[a]	12	13.81[a]	12
28-Apr-06, 1-m shoots	20.24[b]	12	7.87[a]	12	60.78[a]	12	29.18[b]	12	13.06[a]	12
26-May-06	9.86[c]	12	4.48[b]	12	82.80[b]	12	52.68[c]	12	7.84[b]	12
4-Apr-07, 15 to 45-cm shoots	32.73[d]	6	9.03[a]	6	52.40[c]	6	23.12[a]	6	13.00[a]	6
4-Apr-07, 1-m shoots	25.54[a]	2	7.71[a]	2	54.72[c]	2	27.28[b]	2	14.32[a]	2
SEM[5]	1.24		1.07		1.40		1.39		0.72	
Leaves										
1-Jul-05	13.26[a]	12	8.64[ab]	12	76.85[a]	12	37.22[a]	12	9.79[ad]	12
6-Sep-05	13.40[a]	12	9.31[abcd]	12	71.44[bc]	12	31.75[b]	12	9.14[a]	12
12-Nov-05	14.71[b]	12	10.49[e]	12	71.84[c]	12	35.84[ad]	12	8.27[bc]	12
19-Mar-06	16.66[c]	12	9.98[cde]	12	71.77[c]	12	32.27[b]	12	7.64[b]	12
26-May-06	16.12[bc]	12	10.19[de]	12	69.86[bd]	12	34.17[c]	12	9.06[ac]	12
1-Jul-06	15.59[bc]	24	9.15[abc]	24	75.58[a]	24	34.69[cd]	24	8.06b	24
12-Nov-06	19.33[d]	22	8.57[a]	22	70.99[bcd]	22	32.21[b]	22	7.99[b]	22
18-Mar-07	19.14[d]	18	9.68[bcde]	18	70.01[d]	18	31.90[b]	18	10.19[d]	18
11-May-07	21.54[e]	19	8.61[a]	19	70.49[bcd]	19	29.32[e]	19	10.97[e]	19
SEM[5]	0.59		0.51		0.67		0.66		0.34	
Culm[6]										
1-Jul-05	0.56[a]	12	2.45[a]	12	90.82[a]	12	64.21[a]	12	5.40[a]	12
6-Sep-05	-0.08[a]	12	2.24[a]	12	88.45[b]	12	63.61[a]	12	5.38[a]	12
12-Nov-05	0.26[a]	12	2.22[a]	12	90.64[a]	12	64.45[a]	12	4.12[b]	12
19-Mar-06	2.26[b]	12	2.05[a]	12	86.63[c]	12	57.57[b]	12	6.74[c]	12
26-May-06	2.90[bc]	12	1.50[b]	12	88.63[b]	12	63.88[a]	12	7.90[d]	12
1-Jul-06	3.48[c]	24	2.04[b]	24	88.78[b]	24	64.20[a]	24	6.75[c]	24
SEM[5]	0.59		0.51		0.67		0.66		0.34	
F (num df, denom df)	100.79 (12,238)		7.43 (12,238)		145.43 (12,238)		175.29 (12,238)		36.56 (12,236)	
P	< 0.001		< 0.001		< 0.001		< 0.001		< 0.001	

Table 2.2 (Continued)

	Percent (dry-matter basis)[1]									
	P		K		Ca		Mg		S	
Sampling date	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N
Shoots										
28-Apr-06, 15 to 45-cm shoots	0.456[a]	12	3.35[a]	12	0.132	12	0.115[a]	12	0.115[a]	12
28-Apr-06, 1-m shoots	0.373[b]	12	2.87[b]	12	0.085	12	0.098[b]	12	0.098[b]	12
26-May-06	0.202[c]	12	1.59[c]	12	0.092	12	0.063[c]	12	0.063[c]	12
4-Apr-07, 15 to 45-cm shoots	0.482[a]	6	3.03[b]	6	0.104	6	0.106[ab]	6	0.106[ab]	6
4-Apr-07, 1-m shoots	0.371[b]	2	2.47[d]	2	0.075	2	0.071[c]	2	0.071[c]	2
SEM[5]	0.021		0.185		0.072		0.012		0.012	
Leaves										
1-Jul-05	0.169[ab]	12	1.55[a]	12	0.295[a]	12	0.148[a]	12	0.080[a]	12
6-Sep-05	0.148[a]	12	1.20[b]	12	0.470[bc]	12	0.154[a]	12	0.072[a]	12
12-Nov-05	0.151[a]	12	0.78[c]	12	0.542[cd]	12	0.144[a]	12	0.077[a]	12
19-Mar-06	0.148[a]	12	0.48[d]	12	0.607[de]	12	0.142[a]	12	0.077[a]	12
26-May-06	0.171[ab]	12	0.90[ce]	12	0.657[e]	12	0.142[a]	12	0.081[a]	12
1-Jul-06	0.163[a]	24	1.27[b]	24	0.360[a]	24	0.153[a]	24	0.093[b]	24
12-Nov-06	0.185[b]	22	0.98[e]	22	0.420[b]	22	0.188[b]	22	0.103[c]	22
18-Mar-07	0.153[a]	18	0.44[d]	18	0.576[d]	18	0.184[b]	18	0.101[bc]	18
11-May-07	0.207[c]	19	1.28[b]	19	0.329[a]	19	0.156[a]	19	0.151[d]	19
SEM[5]	0.0105		0.091		0.035		0.0079		0.0057	
Culm[6]										
1-Jul-05	0.088[a]	12	0.651[a]	12	0.071	12	0.030	12	0.019	12
6-Sep-05	0.112[b]	12	0.586[ab]	12	0.070	12	0.036	12	0.028	12
12-Nov-05	0.127[b]	12	0.435[b]	12	0.078	12	0.039	12	0.018	12
19-Mar-06	---	---	---	---	---	---	---	---	---	---
26-May-06	---	---	---	---	---	---	---	---	---	---
1-Jul-06	---	---	---	---	---	---	---	---	---	---
SEM[5]	0.0105		0.091		0.035		0.0079		0.0057	
F (num df, denom df)	55.52 (12,189)		50.51 (12,189)		15.29 (12,189)		10.67 (12,189)		22.49 (12,189)	
P	< 0.001		< 0.001		< 0.001		< 0.001		< 0.001	

Table 2.2 (Continued)

	Parts per million (dry-matter basis)[1]									
	Fe		Mn		Zn		Cu		B	
Sampling date	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N
Shoots										
28-Apr-06, 15 to 45-cm shoots	30.24^{a}	12	101.94^{ab}	12	43.76^{a}	12	9.25^{a}	12	4.95^{a}	12
28-Apr-06, 1-m shoots	26.65^{a}	12	76.02^{a}	12	30.09^{b}	12	8.50^{a}	12	3.95^{a}	12
26-May-06	15.65^{b}	12	71.60^{a}	12	16.26^{c}	12	5.59^{b}	12	2.03^{b}	12
4-Apr-07, 15 to 45-cm shoots	33.87^{a}	6	201.73^{b}	6	49.88^{d}	6	12.17^{c}	6	4.61^{a}	6
4-Apr-07, 1-m shoots	26.24^{ab}	2	139.05^{ab}	2	33.50^{b}	2	10.04^{ac}	2	3.59^{ab}	2
SEM[5]	7.16		91.35		3.47		1.19		1.34	
Leaves										
1-Jul-05	61.74^{ab}	12	209.52^{a}	12	10.09^{ab}	12	2.25^{a}	12	5.45^{a}	12
6-Sep-05	55.40^{a}	12	261.77^{ab}	12	7.59^{a}	12	3.25^{ad}	12	11.03^{b}	12
12-Nov-05	54.99^{a}	12	378.35^{cd}	12	11.26^{b}	12	0.25^{b}	12	4.78^{a}	12
19-Mar-06	59.57^{a}	12	454.85^{d}	12	18.68^{c}	12	2.09^{a}	12	7.37^{c}	12
26-May-06	55.66^{a}	12	448.82^{d}	12	19.19^{c}	12	5.45^{c}	12	8.78^{c}	12
1-Jul-06	60.84^{a}	24	262.54^{ab}	24	18.11^{c}	24	5.98^{c}	24	5.29^{a}	24
12-Nov-06	66.42^{b}	22	311.06^{bc}	22	18.50^{c}	22	3.52^{d}	22	4.67^{a}	22
18-Mar-07	111.57^{c}	18	714.56^{e}	18	37.63^{d}	18	3.67^{d}	18	8.15c	18
11-May-07	82.41^{d}	19	1000.99^{f}	19	41.44^{e}	19	8.03^{e}	19	8.69^{c}	19
SEM[5]	3.52		44.89		1.71		0.59		0.66	
Culm[6]										
1-Jul-05	8.655	12	59.270	12	10.34^{a}	12	0.75^{a}	12	0.95	12
6-Sep-05	12.238	12	72.020	12	14.84^{b}	12	2.67^{b}	12	1.70	12
12-Nov-05	10.655	12	83.936	12	17.84^{b}	12	0.84^{a}	12	1.12	12
19-Mar-06	---	---	---	---	---	---	---	---	---	---
26-May-06	---	---	---	---	---	---	---	---	---	---
1-Jul-06	---	---	---	---	---	---	---	---	---	---
SEM[5]	3.52		44.89		1.71		0.59		0.66	
F (num df, denom df)	40.80 (12,189)		33.77 (12,189)		73.19 (12,189)		19.28 (12,189)		13.04 (12,189)	
P	< 0.001		< 0.001		< 0.001		< 0.001		< 0.001	

[1]Lettered superscripts indicate significant differences within columns ($P < 0.05$).
[2]CP = crude protein
[3]NDF = neutral-detergent fiber
[4]ADF = acid-detergent fiber
[5]Maximum standard error of the mean, by plant part and sampling date
[6]Central, woody stem of bamboo
Notes: Samples were taken at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2007. Least-square means are adjusted for effects of ramet age via mixed-model repeated-measures ANOVA (PROC MIXED; SAS Institute, 2012), with subplot sampled as the repeated unit and sampling date as the main (random) effect.

Table 2.3 Nutrient concentration of bamboo by sampling date and plant part: *Phyllostachys glauca.*

	Percent (dry-matter basis)[1]															
	CP[2]		Ash		NDF[3]		ADF[4]		Lipid		P		K		Ca	
Sampling date	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N
Shoots																
28-Apr-06, 15 to 45-cm shoots	16.99^{a}	12	9.19^{a}	12	63.80^{a}	12	30.96^{a}	12	11.77	12	0.325^{a}	12	2.65	12	0.141	12
28-Apr-06, 1-m shoots	13.45^{b}	12	8.12^{b}	12	61.29^{b}	12	34.93^{b}	12	12.62	12	0.287^{b}	12	2.47	12	0.096	12
SEM[5]	0.50		0.47		1.11		1.19		0.40		0.013		0.095		0.038	
Leaves																
6-Sep-05	15.57^{a}	12	11.70^{a}	12	68.75^{a}	12	32.29^{abc}	12	8.56^{a}	12	0.118^{a}	12	0.84^{a}	12	0.497^{ad}	12
12-Nov-05	13.73^{b}	12	12.83^{b}	12	73.55^{c}	12	38.91^{d}	12	7.27^{b}	12	0.133^{ac}	12	0.85^{a}	12	0.440^{ab}	12
19-Mar-06	15.94^{a}	12	13.95^{c}	12	69.66^{abc}	12	33.38^{bc}	12	7.80^{ab}	12	0.125^{a}	12	0.52^{b}	12	0.497^{ad}	12
26-May-06	18.77^{d}	12	8.46^{d}	12	71.90^{bc}	12	32.58^{bc}	12	8.49^{a}	12	0.179^{bd}	12	1.23^{cd}	12	0.388^{b}	12
1-Jul-06	17.49^{c}	24	8.96^{d}	24	73.36^{c}	24	34.44^{c}	24	9.38^{c}	24	0.156^{bc}	24	1.07^{c}	24	0.315^{c}	24
12-Nov-06	17.71^{c}	23	10.67^{e}	23	69.86^{ab}	23	33.15^{bc}	23	8.30^{a}	23	0.168^{b}	23	0.69^{ab}	23	0.529^{d}	23
18-Mar-07	21.01^{e}	11	11.21^{ae}	11	68.08^{a}	11	31.38^{ab}	11	9.93^{c}	11	0.199^{d}	11	0.65^{ab}	11	0.462^{abd}	11
11-May-07	22.33^{f}	20	8.85^{d}	20	72.33^{c}	20	29.47^{a}	20	11.12^{d}	20	0.250^{e}	20	1.43	20	0.468^{abd}	20
SEM[5]	0.50		0.47		1.11		1.19		0.40		0.013		0.095		0.038	
Culm[6]																
6-Sep-05	0.64^{ab}	12	2.93^{a}	12	88.65^{a}	12	67.21^{a}	12	5.68^{a}	12	0.110	12	0.454	12	0.048	12
12-Nov-05	-0.20^{a}	12	2.94^{a}	12	92.51^{b}	12	71.13^{b}	12	3.81^{b}	12	0.133	12	0.393	12	0.049	12
19-Mar-06	1.21^{b}	12	2.93^{a}	12	87.30^{a}	12	63.40^{c}	12	6.47^{ac}	12	---	---	---	---	---	---
26-May-06	2.49^{c}	12	0.98^{b}	12	91.67^{b}	12	68.66^{ab}	12	7.02^{c}	12	---	---	---	---	---	---
1-Jul-06	2.57^{c}	24	2.27^{a}	24	91.61^{b}	24	68.63^{a}	24	6.99^{c}	24	---	---	---	---	---	---
SEM[5]	0.50		0.47		1.11		1.19		0.40		0.013		0.095		0.038	
F (num df, denom df)	31.24 (8,194)		12.49 (8,194)		8.90 (8,194)		10.62 (8,194)		14.51 (8,193)		9.35 (8,145)		13.24 (8,145)		8.12 (8,145)	
P	< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001	

Table 2.3 (Continued)

	% (dry-matter basis)[1]				Parts per million (dry-matter basis) [1]									
	Mg		S		Fe		Mn		Zn		Cu		B	
Sampling date	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N
Shoots														
28-Apr-06, 15 to 45-cm shoots	0.109	12	0.120	12	28.62	12	70.43	12	37.02^{a}	12	8.54^{a}	12	0.82	12
28-Apr-06, 1-m shoots	0.093	12	0.084	12	21.28	12	40.18	12	22.52^{b}	12	6.21^{b}	12	0.07	12
SEM[5]	0.013		0.019		3.60		62.51		2.22		0.48		1.46	
Leaves														
6-Sep-05	0.151^{a}	12	0.118^{a}	12	43.28^{a}	12	207.68^{ab}	12	3.77^{a}	12	2.71^{a}	12	4.82^{a}	12
12-Nov-05	0.156^{ab}	12	0.071^{b}	12	54.70^{bc}	12	247.84^{ab}	12	7.52^{ab}	12	2.71^{a}	12	1.24^{b}	12
19-Mar-06	0.146^{a}	12	0.092^{ab}	12	68.53^{d}	12	409.34^{c}	12	9.94^{b}	12	2.87^{a}	12	4.74^{a}	12
26-May-06	0.196^{c}	12	0.104^{ab}	12	53.39^{b}	12	343.22^{bc}	12	17.33^{c}	12	5.94^{b}	12	9.15^{cd}	12
1-Jul-06	0.176^{bc}	24	0.098^{ab}	24	52.63^{b}	24	202.66^{a}	24	15.43^{c}	24	5.24^{bc}	24	6.78^{ac}	24
12-Nov-06	0.233^{d}	23	0.099^{ab}	23	61.41^{c}	23	551.66^{d}	23	16.57^{c}	23	3.61^{ad}	23	5.00^{a}	23
18-Mar-07	0.185^{bc}	11	0.121^{a}	11	105.05^{f}	11	1038.89^{e}	11	41.91^{d}	11	5.28^{bc}	11	9.59^{cd}	11
11-May-07	0.264^{d}	20	0.226^{c}	20	78.57^{e}	20	1291.57^{f}	20	35.58^{e}	20	4.36^{cd}	20	11.00^{d}	20
SEM[5]	0.013		0.019		3.60		62.51		2.22		0.48		1.46	
Culm[6]														
6-Sep-05	0.039	12	0.021	12	6.62^{a}	12	4.01	12	5.19	12	3.37	12	-1.68	12
12-Nov-05	0.040	12	0.017	12	14.53^{b}	12	15.76	12	9.19	12	3.46	12	-1.84	12
SEM[5]	0.013		0.019		3.60		62.51		2.22		0.48		1.46	
F (num df, denom df)	12.59 (8,145)		5.99 (8,145)		36.89 (8,145)		47.35 (8,145)		36.55 (8,145)		10.17 (8,145)		3.67 (8,145)	
P	< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001	

[1]Lettered superscripts indicate significant differences within columns ($P < 0.05$).
[2]CP = crude protein
[3]NDF = neutral-detergent fiber
[4]ADF = acid-detergent fiber
[5]Maximum standard error of the mean, by plant part and sampling date
[6]Central, woody stem of bamboo
Notes: Samples were taken at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2007. Least-square means are adjusted for effects of ramet age via mixed-model repeated-measures ANOVA (PROC MIXED; SAS Institute, 2012), with subplot sampled as the repeated unit and sampling date as the main (random) effect.

Table 2.4 Nutrient concentration of bamboo by sampling date and plant part: *Phyllostachys rubromarginata.*

	Percent (dry-matter basis)[1]															
	CP[2]		Ash		NDF[3]		ADF[4]		Lipid		P		K		Ca	
Sampling date	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N
Shoots																
28-Apr-06, 15 to 45-cm shoots	13.65^{a}	12	7.87	12	68.58^{a}	12	36.87^{a}	12	11.55	12	0.310^{a}	12	2.49	12	0.109	12
28-Apr-06, 1-m shoots	12.36^{b}	12	7.51	12	64.71^{b}	12	34.35^{b}	12	12.21	12	0.272^{b}	12	2.34	12	0.073	12
SEM[5]	0.42		0.33		0.62		1.00		0.36		0.011		0.102		0.033	
Leaves																
6-Sep-05	14.52^{a}	12	7.99^{a}	12	72.97^{ab}	12	35.29^{a}	12	8.03^{ab}	12	0.129^{ab}	12	0.99^{ac}	12	0.409^{ab}	12
12-Nov-05	12.92^{b}	12	8.16^{a}	12	76.97^{c}	12	40.10^{b}	12	7.59^{a}	12	0.133^{ab}	12	0.92^{ac}	12	0.467^{b}	12
19-Mar-06	15.44^{c}	12	10.09^{b}	12	71.88^{ae}	12	34.42^{ac}	12	7.43^{a}	12	0.124^{a}	12	0.35^{b}	12	0.567^{c}	12
26-May-06	17.17^{d}	12	7.65^{ac}	12	74.46^{b}	12	34.07^{ac}	12	8.00^{ab}	12	0.153^{bc}	12	0.83^{a}	12	0.368^{ad}	12
1-Jul-06	17.27^{d}	24	7.34^{c}	24	75.70^{d}	24	35.20^{a}	24	8.57^{b}	24	0.169^{cd}	24	1.08^{c}	24	0.313^{d}	24
12-Nov-06	17.27^{d}	23	8.07^{a}	23	72.04^{ae}	23	33.80^{ac}	23	7.96^{a}	23	0.176^{d}	23	0.51^{b}	23	0.554^{c}	23
18-Mar-07	20.06^{e}	10	9.37^{b}	10	71.14^{e}	10	32.94^{c}	10	9.39^{c}	10	0.173^{cd}	10	0.35^{b}	10	0.422^{ab}	10
11-May-07	21.98^{f}	20	9.74^{b}	20	71.04^{e}	20	29.99^{d}	20	11.69^{d}	20	0.226^{e}	20	1.77^{d}	20	0.431^{ab}	20
SEM[5]	0.42		0.33		0.62		1.00		0.36		0.011		0.102		0.033	
Culm[6]																
6-Sep-05	0.68^{a}	12	2.56^{a}	12	89.20^{a}	12	67.21^{a}	12	5.12^{a}	12	0.084^{a}	12	0.501	12	0.035	12
12-Nov-05	-0.90^{b}	12	2.56^{a}	12	92.68^{b}	12	67.77^{a}	12	3.80^{b}	12	0.077^{b}	12	0.447	12	0.036	12
19-Mar-06	0.93^{a}	12	1.93^{a}	12	87.49^{c}	12	61.23^{b}	12	5.79^{ac}	12	---	---	---	---	---	---
26-May-06	2.40^{c}	12	0.59^{b}	12	91.60^{bd}	12	66.69^{a}	12	6.43^{c}	12	---	---	---	---	---	---
1-Jul-06	3.08^{c}	23	2.16^{a}	23	90.69^{d}	23	66.71^{a}	23	6.39^{c}	23	---	---	---	---	---	---
SEM[5]	0.42		0.33		0.62		1.00		0.36		0.011		0.102		0.033	
F (num df, denom df)	31.24 (8,194)		12.49 (8,194)		8.90 (8,194)		10.62 (8,194)		14.51 (8,193)		9.35 (8,145)		13.24 (8,145)		8.12 (8,145)	
P	< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001	

Table 2.4 (Continued)

	% (dry-matter basis)[1]				Parts per million (dry-matter basis) [1]									
	Mg		S		Fe		Mn		Zn		Cu		B	
Sampling date	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N
Shoots														
28-Apr-06, 15 to 45-cm shoots	0.080	12	0.097^{a}	12	16.40	12	161.15	12	35.29^{a}	12	7.18^{a}	12	0.61	12
28-Apr-06, 1-m shoots	0.067	12	0.084^{b}	12	13.48	12	123.32	12	23.62^{b}	12	5.93^{b}	12	0.11	12
SEM[5]	0.010		0.006		3.12		92.18		1.82		0.50		0.79	
Leaves														
6-Sep-05	0.117^{a}	12	0.088^{a}	12	39.15^{a}	12	259.90^{a}	12	4.54^{a}	12	3.43^{ae}	12	6.19^{a}	12
12-Nov-05	0.121^{ab}	12	0.087^{a}	12	49.04^{b}	12	333.49^{a}	12	8.98^{b}	12	2.72^{ab}	12	3.02^{b}	12
19-Mar-06	0.100^{a}	12	0.099^{ab}	12	61.73^{cf}	12	755.57^{b}	12	11.21^{b}	12	2.18^{b}	12	6.86^{a}	12
26-May-06	0.116^{a}	12	0.108^{b}	12	54.41^{bcd}	12	595.82^{bc}	12	20.70^{c}	12	6.09^{cd}	12	7.01^{a}	12
1-Jul-06	0.157^{c}	24	0.126^{c}	24	54.66^{bd}	24	536.57^{c}	24	20.20^{c}	24	6.38^{d}	24	6.35^{a}	24
12-Nov-06	0.198^{d}	23	0.136^{d}	23	57.31^{cdf}	23	1092.82^{d}	23	27.79^{d}	23	3.80^{e}	23	6.03^{a}	23
18-Mar-07	0.146^{bc}	10	0.136^{d}	10	93.37^{e}	10	1799.61^{e}	10	41.35^{e}	10	5.95^{cd}	10	10.47^{c}	10
11-May-07	0.236^{e}	20	0.200^{e}	20	63.76^{f}	20	1075.84^{d}	20	34.21^{f}	20	5.16^{c}	20	11.37^{c}	20
SEM[5]	0.010		0.006		3.12		92.18		1.82		0.50		0.79	
Culm[6]														
6-Sep-05	0.010	12	0.027	12	2.40	12	50.82	12	5.71	12	1.76	12	-0.56	12
12-Nov-05	0.008	12	0.027	12	5.90	12	51.07	12	6.54	12	1.18	12	-1.47	12
SEM[5]	0.010		0.006		3.12		92.18		1.82		0.50		0.79	
F (num df, denom df)	12.59 (8,145)		5.99 (8,145)		36.89 (8,145)		47.35 (8,145)		36.55 (8,145)		10.17 (8,145)		3.67 (8,145)	
P	< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001	

[1]Lettered superscripts indicate significant differences within columns ($P < 0.05$).
[2]CP = crude protein
[3]NDF = neutral-detergent fiber
[4]ADF = acid-detergent fiber
[5]Maximum standard error of the mean, by plant part and sampling date
[6]Central, woody stem of bamboo
Notes: Samples were taken at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2007. Least-square means are adjusted for effects of ramet age via mixed-model repeated-measures ANOVA (PROC MIXED; SAS Institute, 2012), with subplot sampled as the repeated unit and sampling date as the main (random) effect.

Table 2.5 Nutrient concentration of bamboo by stage of maturity and plant part: *Phyllostachys aureosulcata*.

	Percent (dry-matter basis)[1]															
	CP[3]		Ash		NDF[4]		ADF[5]		Lipid		P		K		Ca	
Growth stage[2]	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N
Shoots																
1	28.53[a]	18	8.75[a]	18	55.91[a]	18	23.39[a]	18	13.91[a]	18	0.455[a]	18	3.32[a]	18	0.066[a]	18
2	22.69[b]	14	7.56[b]	14	58.09[b]	14	27.88[b]	14	13.68[a]	14	0.365[b]	14	2.87[b]	14	0.019[b]	14
3	12.11[c]	12	4.15[c]	12	80.58[c]	12	51.43[c]	12	8.32[b]	12	0.196[c]	12	1.63[c]	12	0.025[ab]	12
SEM[6]	1.00		0.12		0.93		0.65		0.23		0.0105		0.083		0.0044	
Leaves																
5	14.95[a]	24	8.06[a]	24	75.68[a]	24	35.47[a]	24	9.43[a]	24	0.157[a]	24	1.58[a]	24	0.225[a]	24
6	15.64[a]	12	8.97[b]	12	69.22[b]	12	30.50[b]	12	9.62[a]	12	0.142[ab]	12	1.23[b]	12	0.403[b]	12
7	17.50[b]	24	9.39[b]	24	70.37[b]	24	33.46[c]	24	8.29[b]	24	0.158[a]	24	0.94[c]	24	0.446[c]	24
9	17.88[b]	22	10.12[c]	22	69.87[b]	22	32.35[d]	22	9.24[a]	22	0.140[b]	22	0.50[d]	22	0.571[d]	22
SEM[6]	0.58		0.51		0.55		0.64		0.37		0.0058		0.059		0.0224	
Culm[7]																
5	2.37[a]	24	2.44	24	88.47[a]	24	63.26[a]	24	6.32[a]	24	0.082[a]	12	0.69[a]	12	0.0037	12
6	2.17[a]	12	1.90	12	86.22[b]	12	62.37[a]	12	5.86[a]	12	0.106[b]	12	0.62[ab]	12	0.0029	12
7	2.50[a]	12	1.88	12	88.41[a]	12	63.21[a]	12	4.60[b]	12	0.121[b]	12	0.47[b]	12	0.0112	12
9	4.50[b]	12	1.72	12	84.41[c]	12	56.33[b]	12	7.22[c]	12	---	---	---	---	---	---
SEM[6]	0.52		0.10		0.47		0.89		0.35		0.0122		0.069		0.0019	
F (num df, denom df)	129.76 (5,163)		24.97 (5,163)		266.58 (5,163)		354.78 (5,163)		50.85 (5,163)		122.56 (5,140)		131.00 (5,140)		56.92 (5,140)	
P	< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001	

Table 2.5 (Continued)

	% (dry-matter basis)[1]				Parts per million (dry-matter basis)[1]									
	Mg		S		Fe		Mn		Zn		Cu		B	
Growth stage[2]	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N
Shoots														
1	0.105[a]	18	0.126[a]	18	30.92[a]	18	88.45	18	47.31[a]	18	11.69[a]	18	4.92[a]	18
2	0.091[a]	14	0.110[b]	14	28.79[a]	14	53.81	14	33.92[b]	14	10.70[a]	14	3.94[a]	14
3	0.065[b]	12	0.081[c]	12	19.90[b]	12	53.36	12	21.00[c]	12	7.97[b]	12	2.11[b]	12
SEM[6]	0.0034		0.0034		0.71		10.29		1.03		0.64		0.76	
Leaves														
5	0.141[a]	24	0.100[ab]	24	59.25[a]	24	149.04[a]	24	14.63[a]	24	5.63[a]	24	5.29[a]	24
6	0.152[ab]	12	0.089[a]	12	59.65[a]	12	243.52[b]	12	12.34[a]	12	5.64[a]	12	11.11[b]	12
7	0.154[b]	24	0.102[b]	24	58.21[a]	24	284.33[b]	24	14.58[a]	24	2.75[b]	24	4.75[a]	24
9	0.149[ab]	22	0.095[ab]	22	77.25[b]	22	553.83[c]	22	27.16[b]	22	3.51[b]	22	7.96[c]	22
SEM[6]	0.0091		0.0050		5.41		47.17		2.25		0.62		0.99	
Culm[7]														
5	0.028	12	0.036	12	12.90	12	41.02	12	15.09	12	3.14[a]	12	1.02	12
6	0.034	12	0.046	12	16.48	12	53.77	12	19.59	12	5.06[b]	12	1.77	12
7	0.037	12	0.035	12	14.90	12	65.69	12	22.59	12	3.22[a]	12	1.19	12
SEM[6]	0.0022		0.0028		0.96		5.44		2.70		0.22		0.13	
F (num df, denom df)	5.36 (5,140)		11.59 (5,140)		15.55 (5,140)		41.98 (5,140)		73.19 (5,140)		15.83 (5,140)		19.15 (5,140)	
P	< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001	

[1]Lettered superscripts indicate significant differences within columns ($P < 0.05$).
[2]First-year stages of development: 1 = shoot 15 to 45 cm tall; 2 = shoot ~1m tall; 3 = jointed shoot (maximum height reached, branches unfolded); 5 = 30 days after leaf emergence; 6 = 90 days after leaf emergence; 7 = first freeze (mid-November); 9 = preparation for shoot emergence (March).
[3]CP = crude protein
[4]NDF = neutral-detergent fiber
[5]ADF = acid-detergent fiber
[6]Maximum standard error of the mean, by plant part and sampling date
[7]Central, woody stem of bamboo
Notes: Samples were taken at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and May 2007. Least-square means are adjusted for study year via repeated-measures ANOVA (PROC GLM; SAS Institute, 2012), with subplot sampled as the repeated unit and sampling date as the main effect.

Table 2.6 Nutrient concentration of bamboo by stage of maturity and plant part: *Phyllostachys glauca.*

	Percent (dry-matter basis)[1]															
	CP[3]		Ash		NDF[4]		ADF[5]		Lipid		P		K		Ca	
Growth stage[2]	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N
Shoots																
1	20.45[a]	12	6.55[a]	12	61.43	12	26.72[a]	12	12.71	12	0.352[a]	12	2.67	12	0.171	12
2	16.91[b]	12	5.47[b]	12	58.92	12	30.69[b]	12	13.56	12	0.313[b]	12	2.49	12	0.126	12
SEM[6]	0.83		0.23		2.00		2.97		0.51		0.014		0.121		0.0070	
Leaves																
5	16.64[a]	12	8.44[a]	12	75.43[a]	12	36.21[a]	12	8.72[ab]	12	0.119[a]	12	1.20[a]	12	0.136[a]	12
6	19.02[b]	12	9.06[a]	12	66.39[b]	12	28.05[b]	12	9.49[b]	12	0.145[ab]	12	0.86[b]	12	0.527[b]	12
7	16.91[a]	24	10.39[b]	24	71.21[c]	24	34.40[a]	24	7.91[a]	24	0.150[b]	23	0.80[b]	23	0.483[b]	23
9	19.67[b]	14	11.10[b]	14	67.27[b]	14	29.40[b]	14	9.04[b]	14	0.162[b]	14	0.61[c]	14	0.514[b]	14
SEM[6]	0.73		0.66		0.99		0.74		0.49		0.014		0.060		0.038	
Culm[7]																
5	1.42[a]	12	4.00[a]	12	92.63[a]	12	69.98[a]	12	6.35[a]	12	---	---	---	---	---	---
6	4.10[bc]	12	0.29[b]	12	86.29[b]	12	62.97[b]	12	6.62[a]	12	0.137	12	0.48	12	0.079	12
7	3.25[b]	12	0.30[b]	12	90.15[a]	12	66.89[a]	12	4.75[b]	12	0.159	12	0.41	12	0.079	12
9	4.66[c]	12	0.29[b]	12	84.93[b]	12	59.16[c]	12	7.41[a]	12	---	---	---	---	---	---
SEM[6]	0.42		0.20		2.28		1.74		0.24		0.013		0.065		0.0019	
F (num df, denom df)	16.50 (4,112)		3.96 (4,112)		9.28 (4,112)		11.71 (4,112)		13.52 (4,112)		4.66 (4,89)		7.34 (4,89)		27.80 (4,89)	
P	< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		0.002		< 0.001		< 0.001	

Table 2.6 (Continued)

	% (dry-matter basis)[1]				Parts per million (dry-matter basis)[1]											
	Mg		S		Fe		Mn		Zn		Cu		B			
Growth stage[2]	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N		
Shoots																
1	0.139	12	0.139	12	33.93^{a}	12	285.99	12	51.03^{a}	12	9.48^{a}	12	5.01	12		
2	0.123	12	0.104	12	26.60^{b}	12	255.74	12	36.53^{b}	12	7.15^{b}	12	4.26	12		
SEM[6]	0.0047		0.0067		0.92		9.08		1.27		0.61		0.15			
Leaves																
5	0.114^{a}	12	0.092	12	48.32^{a}	12	-10.66^{a}	12	10.72^{a}	12	6.27^{a}	12	9.74	12		
6	0.180^{bc}	12	0.138	12	48.60^{a}	12	423.24^{b}	12	17.78^{ab}	12	3.65^{b}	12	9.01	12		
7	0.189^{c}	23	0.092	23	59.87^{b}	23	423.97^{b}	23	16.36^{b}	23	3.46^{b}	23	5.23	23		
9	0.171^{b}	14	0.111	14	73.99^{c}	14	664.35^{c}	14	29.12^{c}	14	4.00^{b}	14	9.13	14		
SEM[6]	0.012		0.049		4.50		83.15		5.45		0.58		3.83			
Culm[7]																
6	0.069	12	0.040	12	11.93^{a}	12	219.58	12	19.20	12	4.31	12	2.51	12		
7	0.070	12	0.037	12	19.85^{b}	12	231.33	12	23.20	12	4.40	12	2.34	12		
SEM[6]	0.0028		0.0043		0.87		8.20		1.64		0.26		0.11			
F (num df, denom df)	12.31 (4,89)		1.20 (4,89)		32.83 (4,89)		30.28 (4,89)		15.73 (4,89)		11.40 (4,89)		1.80 (4,89)			
P	< 0.001		0.32		< 0.001		< 0.001		< 0.001		< 0.001		0.14			

[1]Lettered superscripts indicate significant differences within columns (P < 0.05).
[2]First-year stages of development: 1 = shoot 15 to 45 cm tall; 2 = shoot ~1m tall; 3 = jointed shoot (maximum height reached, branches unfolded); 5 = 30 days after leaf emergence; 6 = 90 days after leaf emergence; 7 = first freeze (mid-November); 9 = preparation for shoot emergence (March).
[3]CP = crude protein
[4]NDF = neutral-detergent fiber
[5]ADF = acid-detergent fiber
[6]Maximum standard error of the mean, by plant part and sampling date
[7]Central, woody stem of bamboo
Notes: Samples were taken at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and May 2007. Least-square means are adjusted for study year via repeated-measures ANOVA (PROC GLM; SAS Institute, 2012), with subplot sampled as the repeated unit and sampling date as the main effect.

Table 2.7 Nutrient concentration of bamboo by stage of maturity and plant part: *Phyllostachys rubromarginata.*

	Percent (dry-matter basis)[1]															
	CP[3]		Ash		NDF[4]		ADF[5]		Lipid		P		K		Ca	
Growth stage[2]	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N
Shoots																
1	16.83[a]	12	6.89	12	65.33[a]	12	32.53	12	12.40	12	0.337[a]	12	2.40	12	0.168	12
2	15.54[b]	12	6.53	12	61.46[b]	12	30.01	12	13.06	12	0.299[b]	12	2.26	12	0.132	12
SEM[6]	0.40		0.11		0.77		3.03		0.39		0.0094		0.067		0.0037	
Leaves																
5	17.61[a]	12	6.26[a]	12	76.30[a]	12	35.98[a]	12	8.91	12	0.141[a]	12	1.58[a]	12	0.145[a]	12
6	17.70[b]	12	7.01[b]	12	69.72[b]	12	30.94[b]	12	8.87	12	0.156[ab]	12	0.91[b]	12	0.467[b]	12
7	16.28[c]	24	7.14[b]	24	73.41[c]	24	35.18[a]	24	8.17	23	0.161[b]	23	0.85[b]	23	0.527[c]	23
9	18.44[b]	13	9.14[c]	13	68.96[b]	13	30.64[b]	13	8.54	13	0.151[ab]	12	0.26[c]	12	0.626[d]	12
SEM[6]	0.43		0.29		0.63		0.72		0.60		0.0085		0.085		0.029	
Culm[7]																
5	3.07[ab]	12	3.12[a]	12	90.23[a]	12	67.21[a]	12	6.67[a]	12	---	---	---	---	---	---
6	3.86[b]	12	1.58[b]	12	85.95[b]	12	62.87[b]	12	5.96[a]	12	0.111	12	0.42	12	0.094	12
7	2.28[a]	12	1.58[b]	12	89.44[a]	12	63.43[b]	12	4.64[b]	12	0.104	12	0.36	12	0.095	12
9	4.10[b]	12	0.95[c]	12	84.25[c]	12	56.89[c]	12	6.63[a]	12	---	---	---	---	---	---
SEM[6]	0.41		0.18		0.60		0.62		0.18		0.0063		0.084		0.0050	
F (num df, denom df)	12.35 (4,111)		5.44 (4,111)		34.18 (4,111)		10.08 (4,111)		7.00 (4,111)		4.68 (4,87)		31.99 (4,87)		48.18 (4,87)	
P	< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001	

Table 2.7 (Continued)

	% (dry-matter basis)[1]				Parts per million (dry-matter basis)[1]							
	Mg		S		Fe		Mn		Zn		Cu		B	
Growth stage[2]	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N
Shoots														
1	0.131	12	0.126[a]	12	25.27	12	570.10	12	53.24[a]	12	8.59[a]	12	4.39	12
2	0.118	12	0.114[b]	12	22.35	12	532.27	12	41.58[b]	12	7.34[b]	12	3.89	12
SEM[6]	0.0027		0.0022		1.33		18.36		0.88		0.68		0.22	
Leaves														
5	0.127[a]	12	0.098[a]	12	55.32[ab]	12	-83.02[a]	12	15.51[a]	12	8.50[a]	12	8.28[ab]	12
6	0.168[b]	12	0.118[b]	12	48.02[a]	12	668.85[b]	12	22.49[b]	12	4.84[b]	12	9.97[a]	12
7	0.172[b]	23	0.118[b]	23	57.98[b]	23	748.23[b]	23	27.09[c]	23	4.16[bc]	23	6.78[b]	23
9	0.151[c]	12	0.129[c]	12	70.60[c]	12	1164.52[c]	12	29.16[c]	12	3.59[c]	12	10.64[a]	12
SEM[6]	0.011		0.0066		4.74		113.67		2.52		0.60		1.62	
Culm[7]														
6	0.061	12	0.056	12	11.27	12	459.77	12	23.66	12	3.17	12	3.22	12
7	0.059	12	0.056	12	14.77	12	460.02	12	24.49	12	2.59	12	2.30	12
SEM[6]	0.0017		0.0025		0.60		4.04		1.59		0.26		0.44	
F (num df, denom df)	7.84 (4,87)		7.98 (4,87)		13.15 (4,87)		47.38 (4,87)		26.08 (4,87)		14.49 (4,87)		4.55 (4,87)	
P	< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001	

[1]Lettered superscripts indicate significant differences within columns ($P < 0.05$).
[2]First-year stages of development: 1 = shoot 15 to 45 cm tall; 2 = shoot ~1m tall; 3 = jointed shoot (maximum height reached, branches unfolded); 5 = 30 days after leaf emergence; 6 = 90 days after leaf emergence; 7 = first freeze (mid-November); 9 = preparation for shoot emergence (March).
[3]CP = crude protein
[4]NDF = neutral-detergent fiber
[5]ADF = acid-detergent fiber
[6]Maximum standard error of the mean, by plant part and sampling date
[7]Central, woody stem of bamboo
Notes: Samples were taken at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and May 2007. Least-square means are adjusted for study year via repeated-measures ANOVA (PROC GLM; SAS Institute, 2012), with subplot sampled as the repeated unit and sampling date as the main effect.

Table 2.8 Least-square mean nutrient concentration by ramet age in temperate bamboo.

	Percent (dry-matter basis)[1]															
	CP[2]		Ash		NDF[3]		ADF[4]		Lipid		P		K		Ca	
Ramet age (yr)	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N
PLLAU[5]																
1	10.71	78	5.33	78	80.24	78	48.79	78	7.62	76	0.169	50	0.980	50	0.449	50
2	13.68	7	4.30	7	81.37	7	46.83	7	9.10	7	0.217	7	1.320	7	0.325	7
SEM[6]	0.85		0.47		0.97		1.72		0.49		0.016		0.189		0.037	
F (num df, denom df)	7.52 (1,69)		1.94 (1,69)		1.57 (1,69)		4.10 (1,69)		9.54 (1,67)		10.44 (1,42)		4.29 (1,42)		2.47 (1,42)	
P	0.01		0.17		0.21		0.05		0.003		0.002		0.04		0.12	
PLLGL[5]																
1	10.96	78	6.49	78	79.95	78	49.88	78	7.85	78	0.171	52	0.837	52	0.508	52
2	11.42	10	5.43	10	83.66	10	50.65	10	9.23	9	0.234	9	1.470	9	0.393	9
SEM[6]	0.94		0.50		1.11		1.92		0.25		0.026		0.174		0.038	
F (num df, denom df)	0.69 (1,72)		4.28 (1,72)		25.07 (1,72)		1.42 (1,72)		7.36 (1,71)		12.08 (1,46)		16.04 (1,46)		7.57 (1,46)	
P	0.41		0.04		< 0.001		0.24		0.01		0.001		< 0.001		0.01	
PLLRU[5]																
1	11.57	76	5.73	76	79.74	76	49.14	76	8.40	76	0.184	52	0.982	52	0.508	52
2	10.76	11	5.36	11	83.22	11	49.91	11	8.47	11	0.196	11	1.301	11	0.372	11
SEM[6]	0.88		0.44		1.03		1.80		0.28		0.012		0.114		0.021	
F (num df, denom df)	3.67 (1,71)		1.58 (1,71)		36.58 (1,71)		2.10 (1,71)		0.03 (1,71)		0.60 (1,48)		2.64 (1,48)		15.63 (1,48)	
P	0.06		0.21		< 0.001		0.15		0.86		0.44		0.11		< 0.001	

Table 2.8 (Continued)

	% (dry-matter basis)[1]				Parts per million (dry-matter basis) [1]											
	Mg		S		Fe		Mn		Zn		Cu		B	
Ramet age (yr)	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N
PLLAU[5]														
1	0.164	50	0.106	50	65.31	50	498.30	50	23.75	50	4.66	50	5.83	50
2	0.179	7	0.124	7	72.50	7	781.03	7	31.21	7	5.79	7	6.17	7
SEM[6]	0.005		0.005		8.43		119.43		3.48		0.80		0.61	
F (num df, denom df)	1.65 (1,42)		1.69 (1,42)		0.43 (1,42)		5.03 (1,42)		2.66 (1,42)		1.75 (1,42)		0.19 (1,42)	
P	0.21		0.20		0.52		0.03		0.11		0.19		0.67	
PLLGL[5]														
1	0.243	52	0.131	52	71.47	52	815.49	52	23.14	52	3.69	52	7.13	52
2	0.231	9	0.165	9	48.77	9	617.72	9	19.71	9	4.91	9	6.70	9
SEM[6]	0.023		0.023		3.56		124.03		3.81		0.46		0.70	
F (num df, denom df)	0.34 (1,46)		2.94 (1,46)		12.79 (1,46)		4.21 (1,46)		1.82 (1,46)		5.06 (1,46)		0.20 (1,46)	
P	0.56		0.09		0.001		0.05		0.18		0.03		0.66	
PLLRU[5]														
1	0.214	52	0.135	52	60.17	52	973.18	52	25.22	52	3.96	52	7.57	52
2	0.170	11	0.172	11	47.39	11	712.02	11	20.39	11	5.10	11	6.25	11
SEM[6]	0.010		0.006		3.18		74.73		1.33		0.20		0.47	
F (num df, denom df)	6.25 (1,48)		11.16 (1,48)		7.56 (1,48)		3.33 (1,48)		4.63 (1,48)		13.54 (1,48)		5.54 (1,48)	
P	0.02		0.002		0.01		0.07		0.04		< 0.001		0.02	

[1]Lettered superscripts indicate significant differences within columns ($P < 0.05$).
[2]CP = crude protein
[3]NDF = neutral-detergent fiber
[4]ADF = acid-detergent fiber
[5]PLLAU = Phyllostachys aureosulcata ; PLLGL = P. glauca ; PLLRU = P. rubromarginata
[6]Maximum standard error of the mean, by plant part and sampling date
Notes: Samples were taken at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and May 2007. Means are adjusted for effects of season and plant part (leaves or culm [central, woody stem]) via repeated-measures ANOVA (PROC GLM; SAS Institute, 2012) with subplot sampled as the repeated unit and sampling date as the main effect. Data presented are pooled across plant parts.

Table 2.9 Aboveground disturbance effects on *Phyllostachys glauca* neutral-detergent fiber concentration.

	% NDF (dry-matter basis)[1]	
Disturbance treatment[2]	LS Mean	N
Control	76.05[ab]	72
3%	76.56[a]	75
20%	75.48[b]	75
SEM[3]	1.83	
F (num df, denom df)	5.41 (2,156)	
P	0.005	

[1]Lettered superscripts indicate significant differences within columns ($P < 0.05$).
[2]Aboveground disturbance treatments (administered quarterly) are as follows: control (no bamboo removal), 3% annual removal of live individual ramets, and 20% annual removal.
[3]Maximum standard error of the mean.
Notes: Samples were taken from the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2007. Means are adjusted for other terms in the repeated-measures ANOVA model (PROC GLM; SAS Institute, 2012), with replicate enclosure as the repeated unit, sampling date as the main-plot unit and random effect, disturbance treatment as the subplot unit, and plant part as an additional term in the model. Results are pooled across all plant parts.

Table 2.10 Analysis of Covariance of weather conditions on bamboo nutrient concentration: Correlation and ANCOVA statistics.

Response variable	Independent variable	Covariate[1]	Correlation			Test of homogeneity of slope		ANCOVA results	
			r	N	*P*	F^2 (num df, denom df)	*P*	F^2 (num df, denom df)	*P*
Ash	Sampling date	Temp	-0.205	713	< 0.001	0.95 (3,696)	0.41	10.11 (12,655)	< 0.001
NDF[3]	Sampling date	Temp	0.299	713	< 0.001	0.94 (3,696)	0.42	89.19 (12,655)	< 0.001
ADF[4]	Sampling date	Temp	0.239	713	< 0.001	0.54 (3,696)	0.66	76.85 (12,655)	< 0.001
Ca	Sampling date	Temp	-0.168	559	< 0.001	1.85 (3,542)	0.14	9.81 (12,504)	< 0.001
Ash	Sampling date	Precip	-0.200	713	< 0.001	0.41 (3,696)	0.75	12.30 (12,655)	< 0.001
ADF	Sampling date	Precip	0.108	713	< 0.001	1.36 (3,696)	0.25	82.85 (12,655)	< 0.001
Ca	Sampling date	Precip	-0.212	559	< 0.001	2.05 (3,542)	0.11	16.26 (12,504)	< 0.001
S	Sampling date	Precip	-0.204	559	< 0.001	1.53 (3,542)	0.21	19.93 (12,504)	< 0.001
Zn	Sampling date	Precip	-0.230	559	< 0.001	2.35 (3,542)	0.07	77.04 (12,504)	< 0.001

[1]Temp = Mean monthly temperature; Precip = Total monthly precipitation

[2]F ratio (numerator degrees of freedom, denominator degrees of freedom) for repeated-measures Analysis of Covariance of effects of independent variable

[3]NDF = neutral-detergent fiber

[4]ADF = acid-detergent fiber

Notes: Samples were taken from *Phyllostachys aureosulcata, P. glauca,* and *P. rubromarginata* at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2007. Results are presented only for variables which 1) correlated with either weather condition ($P < 0.05$), and 2) met assumptions of homogeneity of slope for the covariate relationship ($P > 0.05$ for H_0: homogeneous slopes).

Table 2.11 Analysis of Covariance of weather conditions on bamboo nutrient concentration: Adjusted means.

	Percent (dry-matter basis), adjusted for temperature[1]							
	Ash		NDF[2]		ADF[3]		Ca	
Sampling date	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N
Shoots								
28-Apr-06, 15 to 45-cm shoots	8.75^{ab}	36	64.91^{a}	36	31.56^{a}	36	0.147^{a}	36
28-Apr-06, 1-m shoots	7.93^{bc}	36	63.15^{b}	36	33.59^{b}	36	0.105^{ab}	36
26-May-06	4.96^{d}	12	83.15^{c}	12	54.30^{c}	12	0.071^{b}	12
4-Apr-07, 15 to 45-cm shoots	9.51^{ab}	6	53.75^{d}	6	25.68^{d}	6	0.103^{ab}	6
4-Apr-07, 1-m shoots	8.19^{abc}	2	56.07^{d}	2	29.84^{abd}	2	0.073^{ab}	2
SEM[4]	0.19		0.92		1.29		0.0050	
Leaves								
1-Jul-05	9.10^{abc}	12	75.23^{ac}	12	36.98^{abc}	12	0.232^{a}	12
6-Sep-05	9.73^{bcd}	36	68.18^{b}	36	30.33^{b}	36	0.397^{b}	36
12-Nov-05	10.59^{d}	36	75.18^{a}	36	39.21^{ab}	36	0.507^{cd}	35
19-Mar-06	11.45^{e}	36	73.72^{cd}	36	35.74^{ac}	36	0.614^{e}	36
26-May-06	8.84^{ab}	36	71.75^{fg}	36	33.31^{d}	36	0.469^{c}	36
1-Jul-06	8.55^{a}	72	73.07^{de}	72	33.04^{d}	72	0.294^{a}	69
12-Nov-06	9.21^{ab}	68	72.14^{ef}	68	34.14^{d}	68	0.533^{d}	66
18-Mar-07	10.20^{cd}	39	70.90^{g}	39	33.36^{d}	39	0.529^{d}	37
11-May-07	9.04^{ab}	59	71.31^{fg}	59	29.65^{b}	59	0.399^{b}	56
SEM[4]	0.41		0.49		0.41		0.025	
Culm[5]								
1-Jul-05	2.91^{a}	12	89.20^{ac}	12	63.98^{abc}	12	0.008^{ab}	12
6-Sep-05	2.64^{a}	36	85.89^{b}	36	63.23^{a}	36	-0.011^{a}	36
12-Nov-05	2.67^{a}	36	93.01^{d}	36	68.72^{d}	36	0.078^{b}	36
19-Mar-06	2.41^{a}	36	89.76^{ac}	36	63.12^{ab}	36		
26-May-06	1.10^{b}	36	90.31^{c}	36	66.12^{c}	36		
1-Jul-06	2.21^{a}	71	88.56^{a}	71	64.78^{bc}	71		
SEM[4]	0.16		0.44		0.55		0.0018	

Table 2.11 (Continued)

	Concentration[6] (dry-matter basis), adjusted for precipitation									
	Ash		ADF		Ca		S		Zn	
Sampling date	LS Mean	N	LS Mean	N	LS Mean	N	LS Mean	N		
Shoots										
28-Apr-06, 15 to 45-cm shoots	9.18[a]	36	29.80[a]	36	0.155[a]	36	0.133[a]	36	35.79[a]	36
28-Apr-06, 1-m shoots	8.36[b]	36	31.83[b]	36	0.112[ab]	36	0.111[b]	36	22.51[b]	36
26-May-06	5.50[c]	12	53.51[c]	12	0.113[ab]	12	0.102[bc]	12	8.33[c]	12
4-Apr-07, 15 to 45-cm shoots	8.22[ab]	6	27.47[a]	6	0.012[b]	6	0.068[cd]	6	53.33[d]	6
4-Apr-07, 1-m shoots	6.91[bc]	2	31.60[ab]	2	-0.017[b]	2	0.032[d]	2	37.02[a]	2
SEM[4]	0.19		1.29		0.0050		0.0056		2.50	
Leaves										
1-Jul-05	9.15[abc]	12	39.04[a]	12	0.285[a]	12	0.097[a]	12	5.38[a]	12
6-Sep-05	11.07[e]	36	30.44[b]	36	0.539[ab]	36	0.151[b]	36	-3.05[b]	36
12-Nov-05	9.36[cd]	36	40.48[a]	36	0.410[cd]	35	0.031[c]	35	16.68[ce]	35
19-Mar-06	11.56[e]	36	32.95[c]	36	0.566[a]	36	0.099[a]	36	12.29[d]	36
26-May-06	9.36[bd]	36	32.66[c]	36	0.510[ab]	36	0.121[d]	36	14.90[cd]	36
1-Jul-06	8.37[a]	72	35.09[d]	72	0.323[a]	69	0.101[a]	69	18.45[e]	69
12-Nov-06	8.95[bc]	68	33.47[c]	68	0.493[b]	66	0.106[ad]	66	22.02[f]	66
18-Mar-07	8.95[abc]	39	34.79[cd]	39	0.435[bc]	37	0.068[e]	37	45.55[h]	37
11-May-07	8.53[ab]	59	30.69[b]	59	0.373[d]	56	0.172[b]	56	39.95[g]	56
SEM[4]	0.41		0.41		0.025		0.016		1.71	
Culm[5]										
1-Jul-05	2.96[ad]	12	66.03[a]	12	0.061[ab]	12	0.036[a]	12	5.63[a]	12
6-Sep-05	3.98[d]	36	63.34[b]	36	0.131[a]	36	0.084[b]	36	0.23[b]	36
12-Nov-05	1.45[b]	36	69.98[c]	36	-0.019[b]	36	-0.027[c]	36	18.66[c]	36
19-Mar-06	2.53[ac]	36	60.33[d]	36						
26-May-06	1.62[b]	36	65.46[a]	36						
1-Jul-06	2.04[bc]	71	66.83[a]	71						
SEM[4]	0.16		0.55		0.0018		0.0028		1.18	

[1]Lettered superscripts indicate significant differences within columns ($P < 0.05$).
[2]NDF = neutral-detergent fiber
[3]ADF = acid-detergent fiber
[4]Maximum standard error of the mean, by plant part and sampling date
[5]Central, woody stem
[6]Concentration of Ash, ADF, Ca, and S given in %; concentration of Zn given in ppm
Notes: Samples were taken from the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2007. Least-square means are adjusted for other terms in a repeated-measures ANCOVA, with subplot as the repeated unit, ramet cohort and sampling date as main effects, and plant part and bamboo species (*Phyllostachys aureosulcata, P. glauca,* and *P. rubromarginata*) as additional terms in the model.

Table 2.12 Annual soil tests and fertility regime.

				Extractable nutrients (kg/ha)						Nutrient appication (kg/ha/yr)			
Species[1]	Date	pH	CEC[2]	P	K	Ca	Mg	Zn	Na	Lime	N	P205	K20
PLLAU	May 2005	6.2	6.7	62.5	119.3	1847	93.2	2.16	63.64	0	68	34	68
	Oct 2006	5.1	6.7	106.8	181.8	1323	126.1	4.77	78.41	5114	68	0	0
	Oct 2007	4.8	8.1	314.8	662.5	1433	150.0	7.50	103.41	6818	68	0	0
PLLGL	May 2005	6.2	6.7	60.2	108.0	1716	95.5	2.50	29.55	0	68	34	68
	Oct 2006	5.1	7.6	129.5	206.8	1476	158.0	5.80	93.18	6818	68	0	0
	Oct 2007	4.6	8.1	321.6	606.8	1366	200.0	7.16	120.45	6818	68	0	0
PLLRU	May 2005	5.8	6.4	77.3	137.5	1303	98.9	2.61	13.64	5114	68	34	34
	Oct 2006	4.7	7.0	205.7	280.7	1036	126.1	5.34	92.05	6818	68	0	0
	Oct 2007	4.5	9.3	590.9	685.2	1681	193.2	6.36	107.95	6818	68	0	0

[1]PLLAU = *Phyllostachys aureosulcata*; PLLGL = *P. glauca*; PLLRU = *P. rubromarginata*.
[2]Cation-exchange capacity, cmol H+/kg
Notes: Soil samples were taken in October of each year from 0.4-ha monoculture bamboo plots at the Shelby County AgriCenter, Memphis, Tennessee, USA. Two locations were sampled per replicate enclosure (8 locations per plot), and pooled by bamboo species for analysis at the Mississippi State University Cooperative Extension Service (MCES) Soil Testing Laboratory. Subsequent fertilizer application in November and January/February of each year was performed according to MCES recommendations for temperate forage grasses.

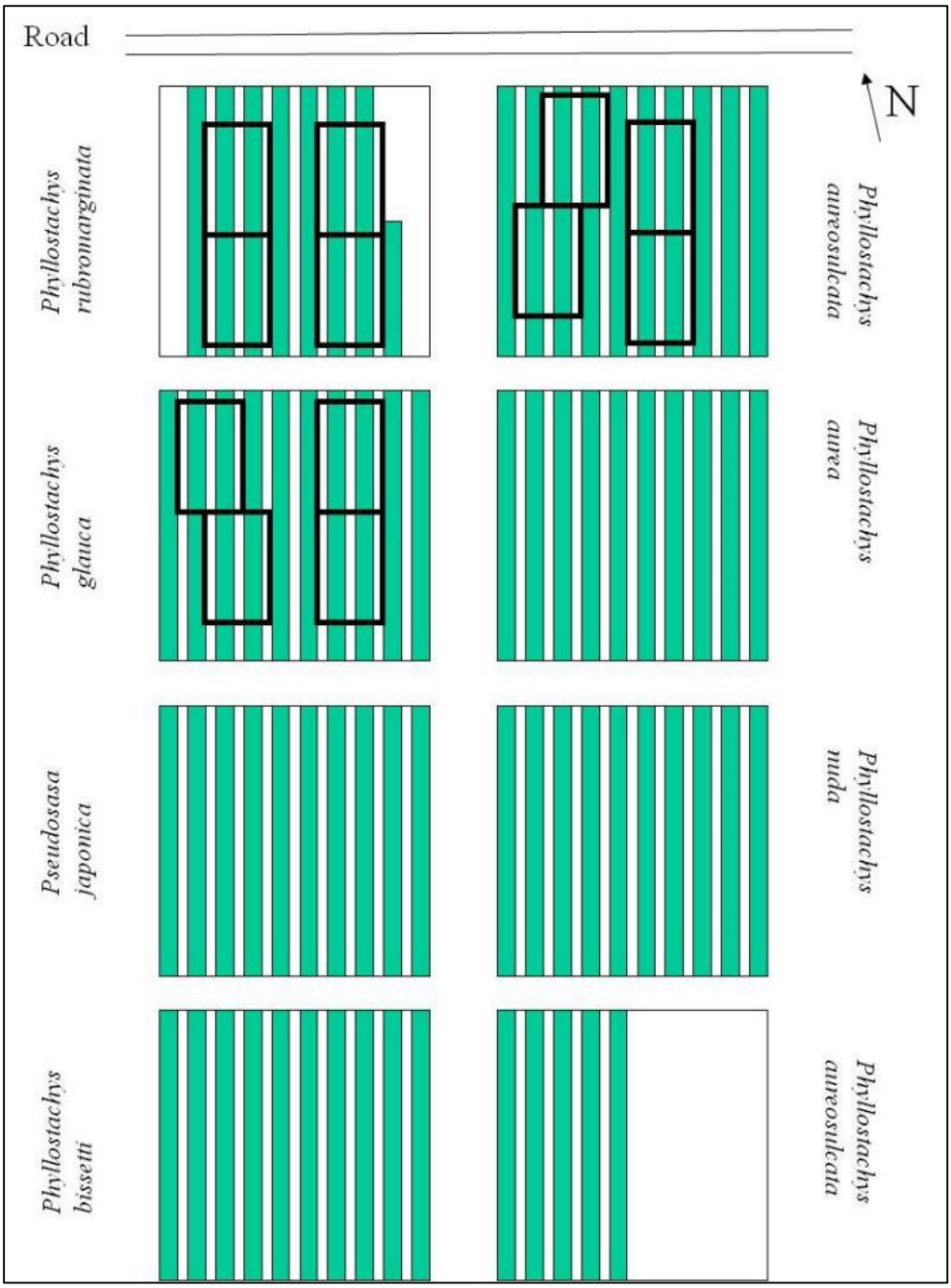

Figure 2.1 Schematic of research plots: Overall layout.

Memphis Zoo-operated browse farm at Shelby County AgriCenter, Memphis, TN. Eight 0.4-ha monoculture plots were planted with 7 bamboo species in 10 rows per plot. Bamboo growth is indicated by green-shaded areas, with mowed aisles (in white) between each row. Experimental enclosures are indicated with black rectangles within each of 3 bamboo species.

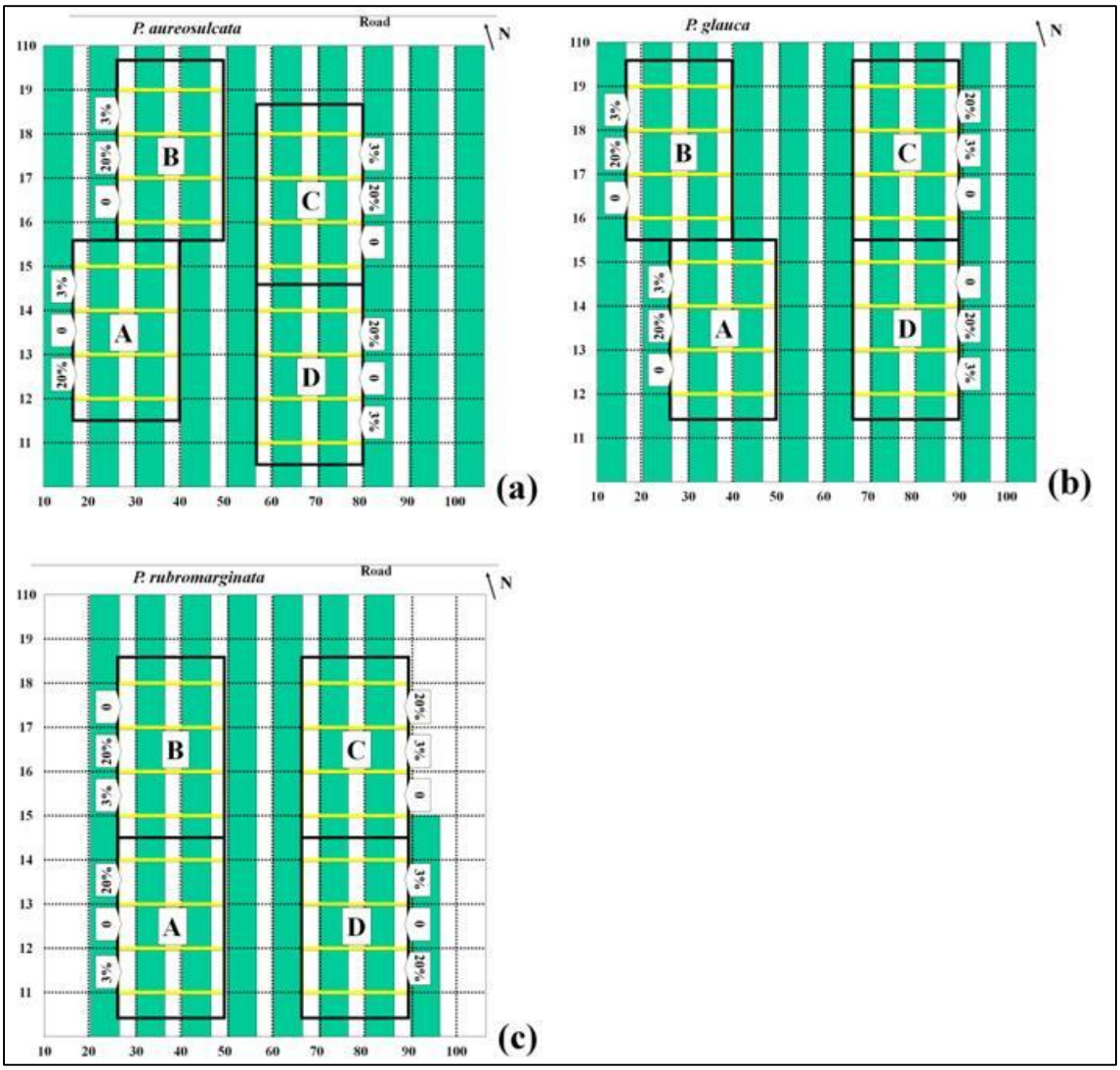

Figure 2.2 Schematic of research plots: Individual bamboo plots.

(a) *Phyllostachys aureosulcata*
(b) *Phyllostachys glauca*
(c) *Phyllostachys rubromarginata*

Within each monoculture plot, a sampling grid (10 x 10, 6-m line spacing) was established (indicated by dashed lines), with numbered flags at intersections to mark location. Replicate enclosures are indicated by black rectangles and letters, and subplots are indicated in yellow. Three disturbance treatments were randomly applied to each enclosure (1 treatment/subplot), and are indicated to the side of each suplot: control (0 bamboo removal), 3% annual removal of live ramets, and 20% annual removal.

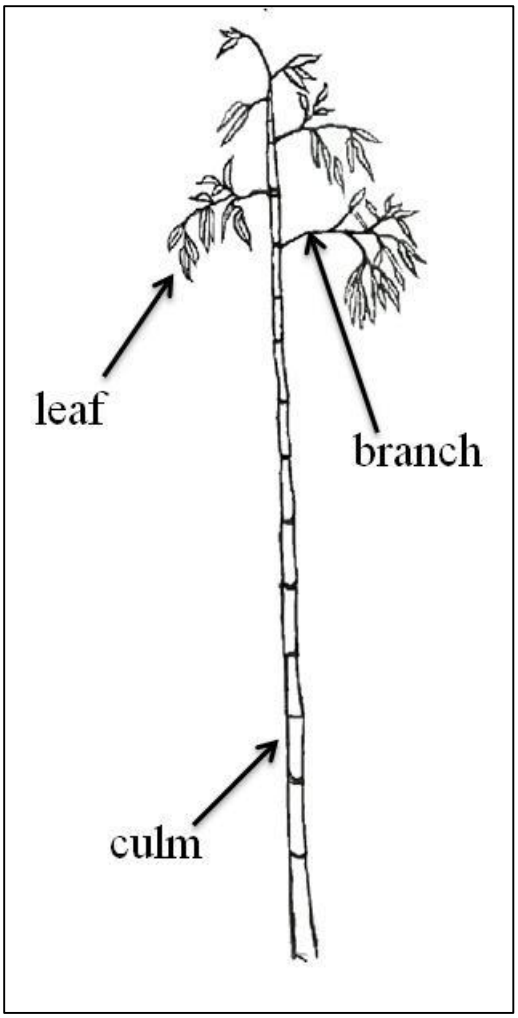

Figure 2.3 Anatomical divisions of *Phyllostachys* bamboo.

Culm is the central support of each ramet, arising directly from a belowground rhizome and divided into hollow cells sectioned off by nodes (horizontal marks). Branches project laterally from nodes, and leaves grow on the distal half of branches.

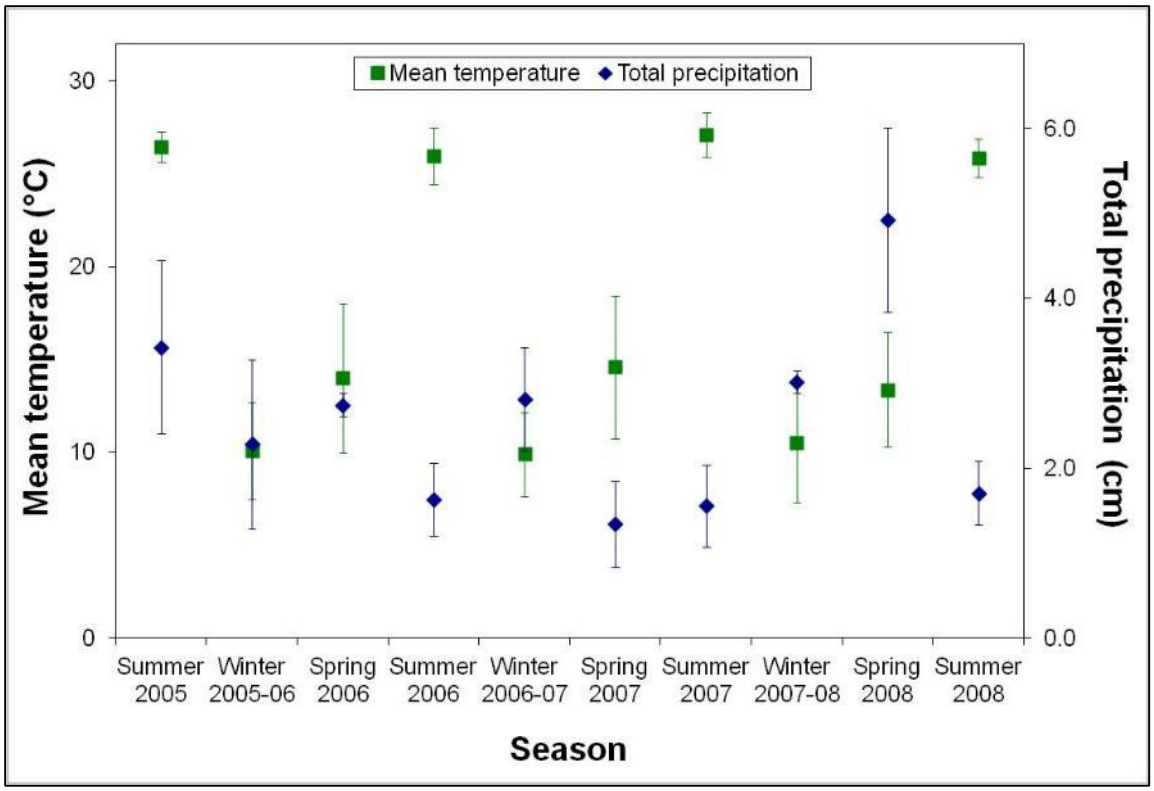

Figure 2.4 Weather data for study period.

Data are taken from a NOAA weather station located at Shelby County AgriCenter, Memphis, Tennessee, USA (35° 7'47"N, 89°48'13"W), 2.5 kilometers from the study site. Mean monthly temperature and total monthly precipitation are averaged by season (Spring = February through May; Summer = June through September; Winter = October through January). Bars indicate standard error.

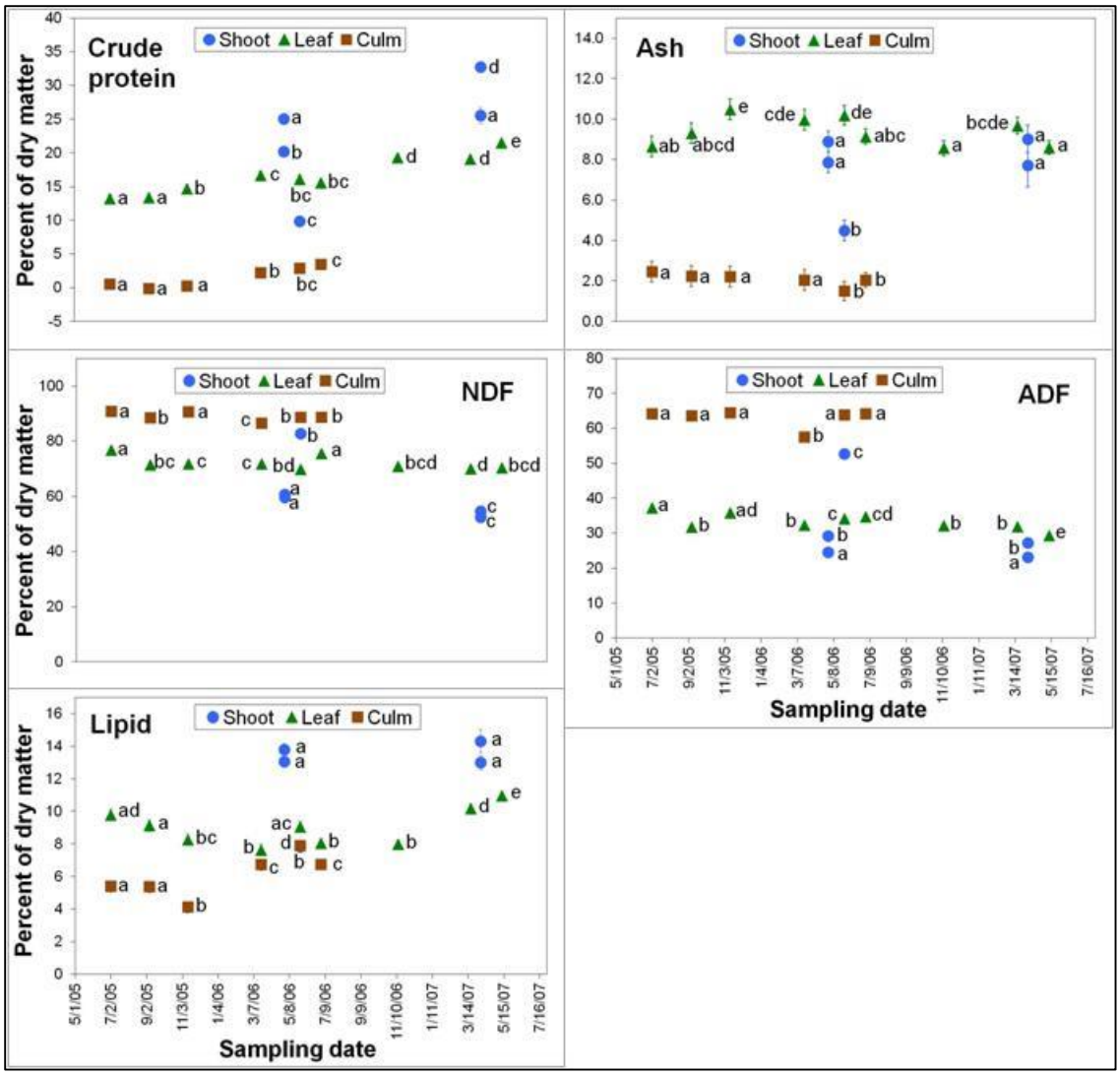

Figure 2.5 Nutrient concentration of bamboo by sampling date: *Phyllostachys aureosulcata*.

Bamboo was sampled from the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and May 2007. Least-square means are adjusted for effects of ramet age via mixed-model repeated-measures ANOVA (PROC MIXED; SAS Institute, 2012), separated by plant part, with subplot as the repeated unit. Means for shoots, leaves, and culm (central, woody stalk) are presented separately. Letters indicate within-part differences across stages of development ($P < 0.05$); bars indicate standard error.

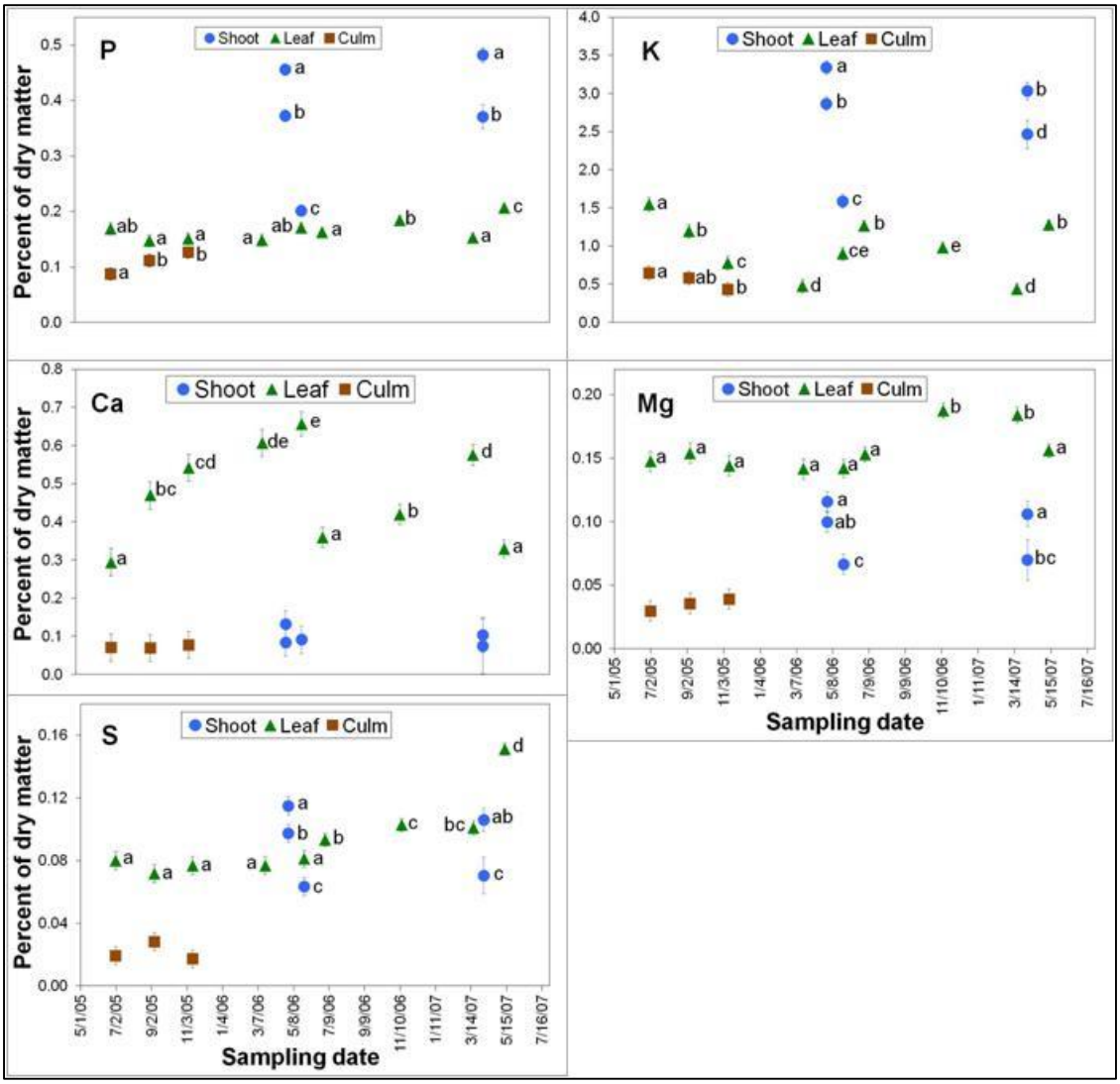

Figure 2.5 (Continued)

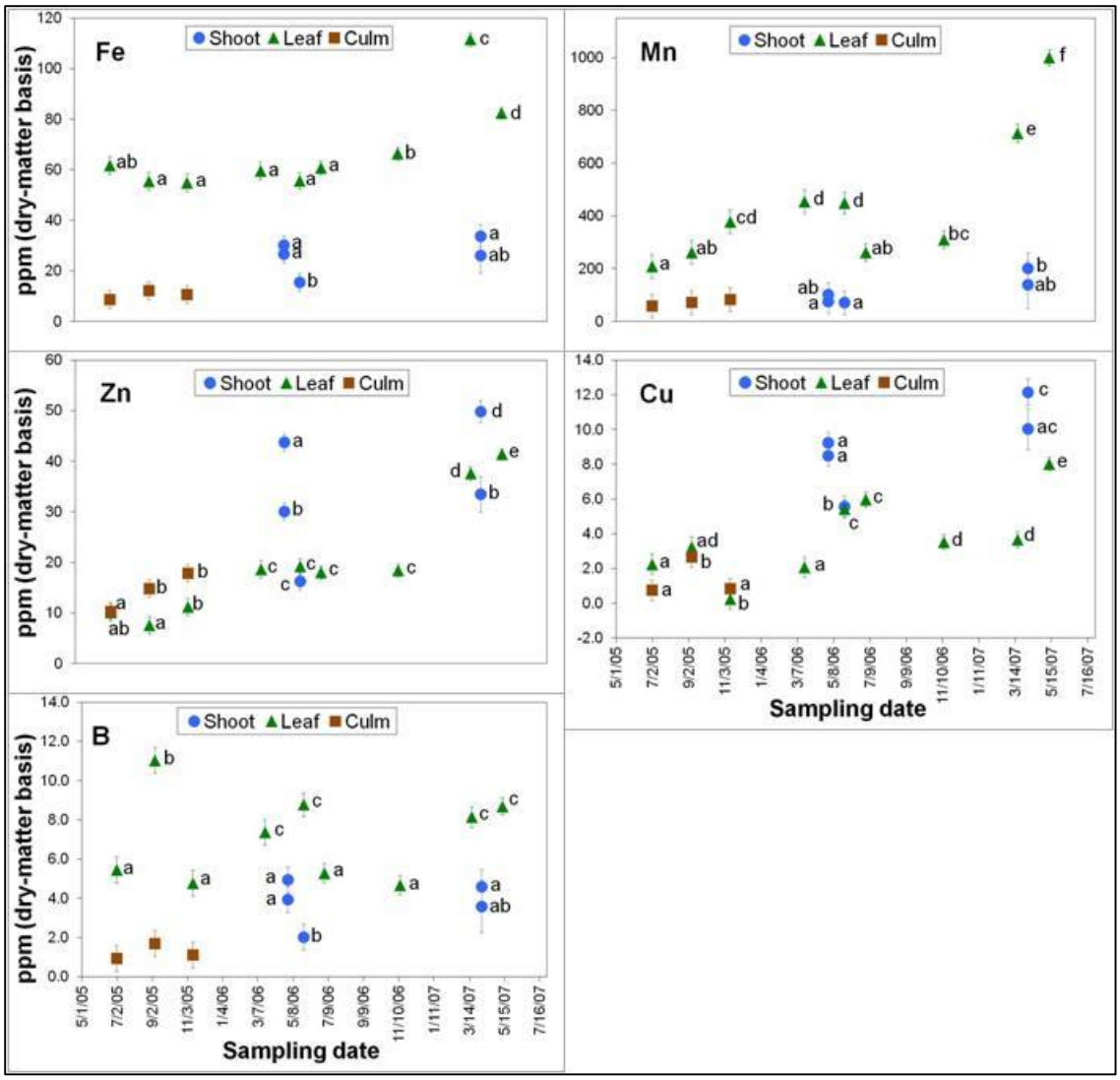

Figure 2.5 (Continued)

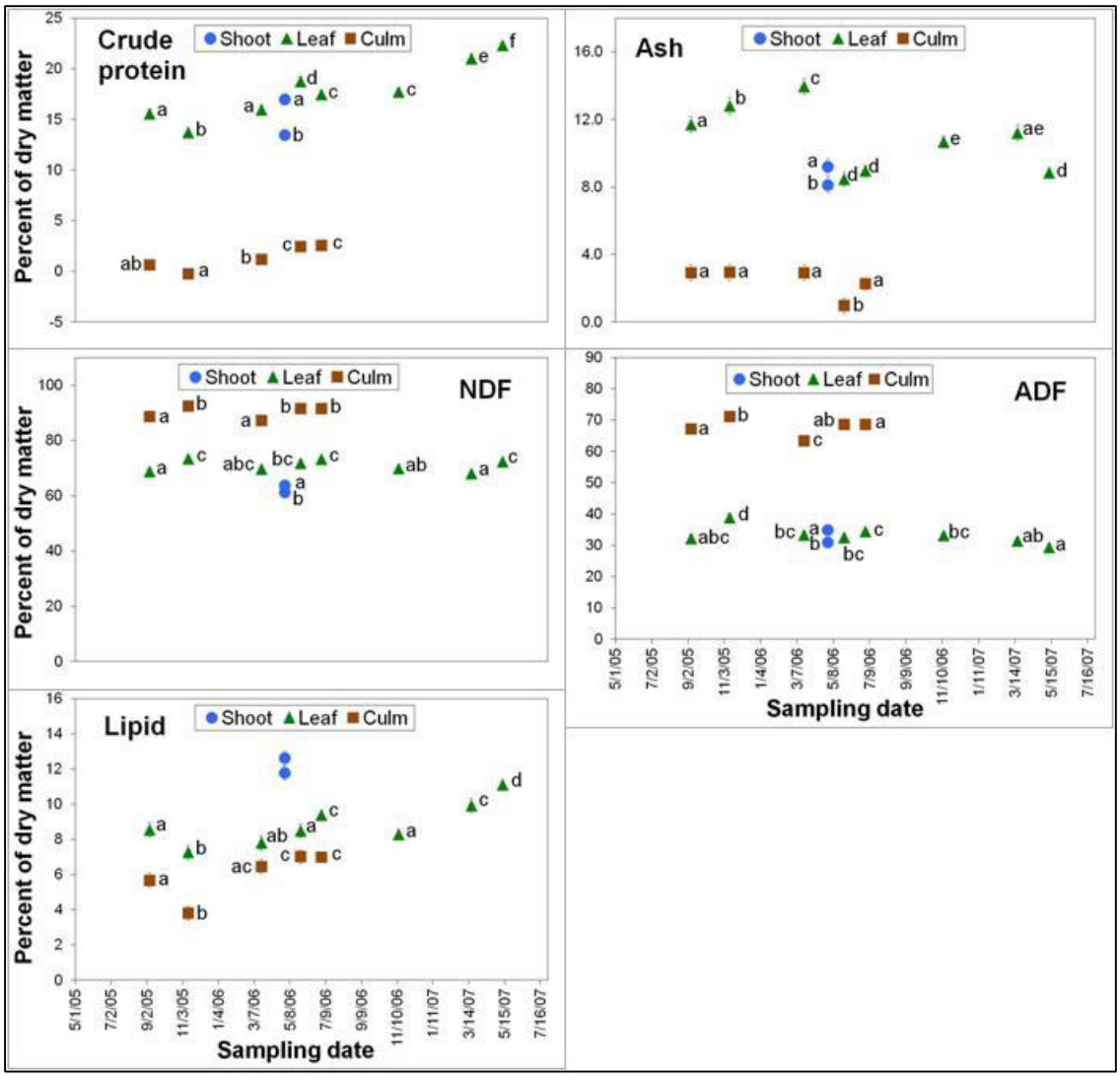

Figure 2.6 Nutrient concentration of bamboo by sampling date: *Phyllostachys glauca*.

Bamboo was sampled from the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and May 2007. Least-square means are adjusted for effects of ramet age via mixed-model repeated-measures ANOVA (PROC MIXED; SAS Institute, 2012), separated by plant part, with subplot as the repeated unit. Means for shoots, leaves, and culm (central, woody stalk) are presented separately. Letters indicate within-part differences across stages of development ($P < 0.05$); bars indicate standard error.

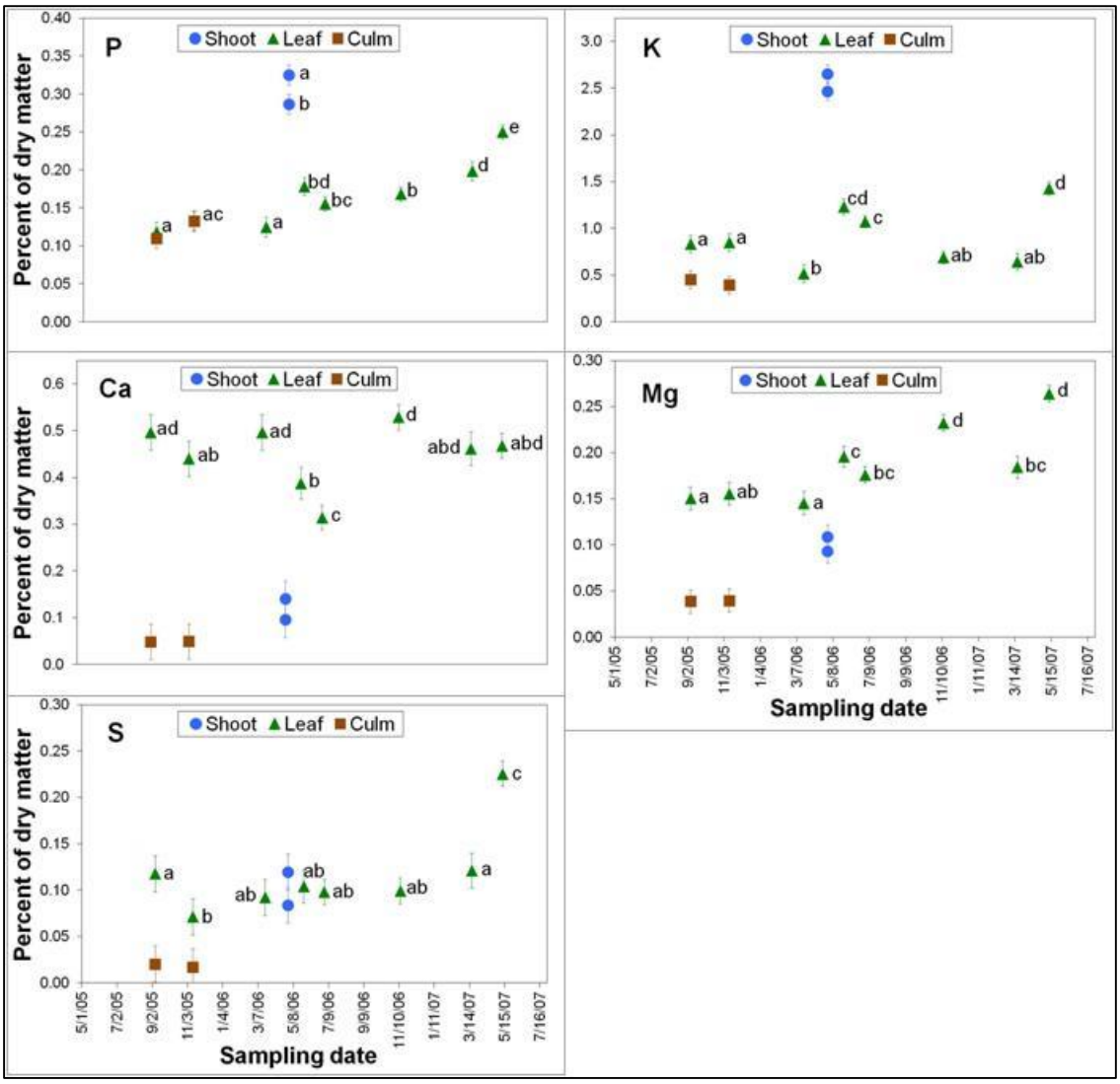

Figure 2.6 (Continued)

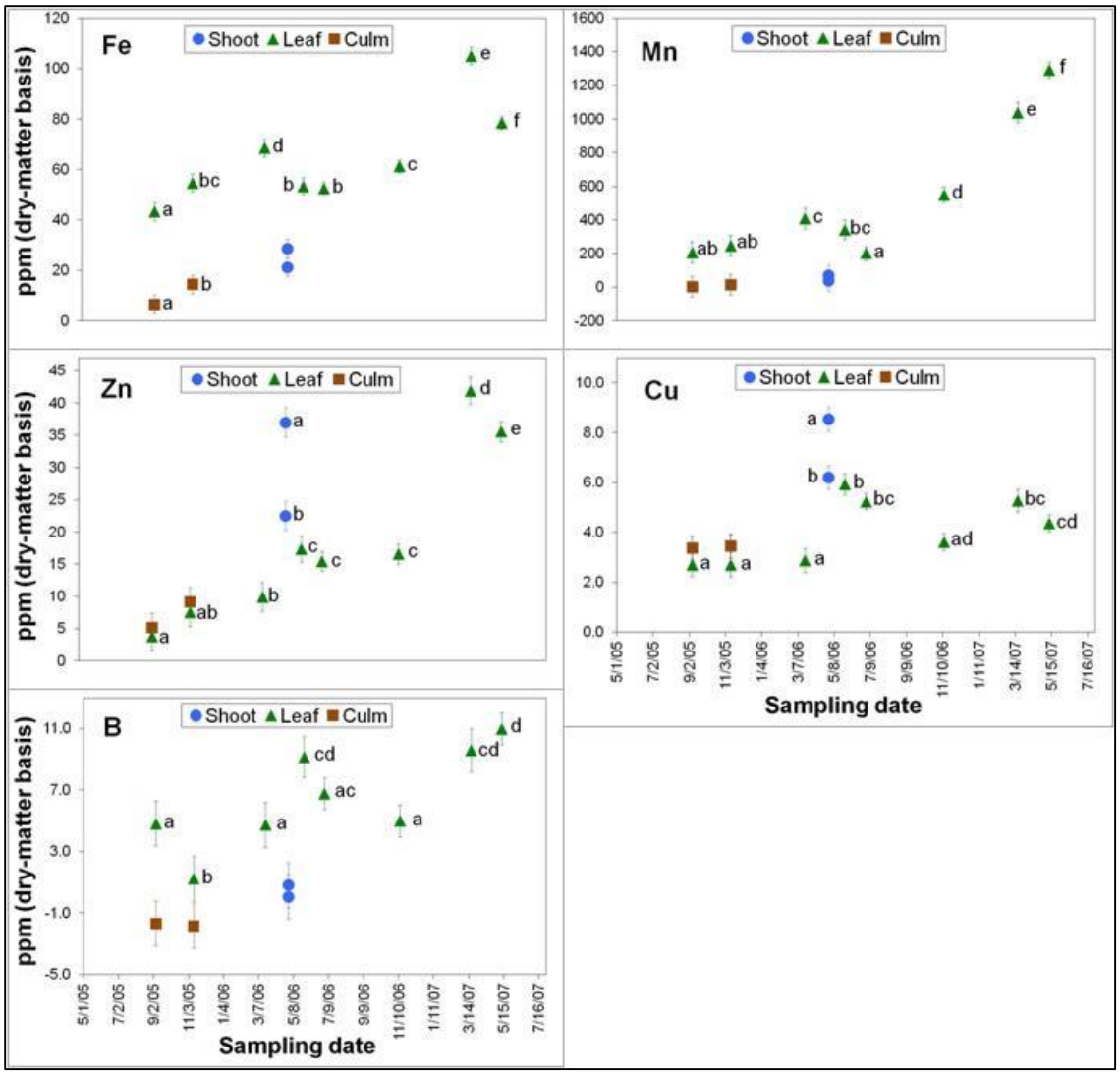

Figure 2.6 (Continued)

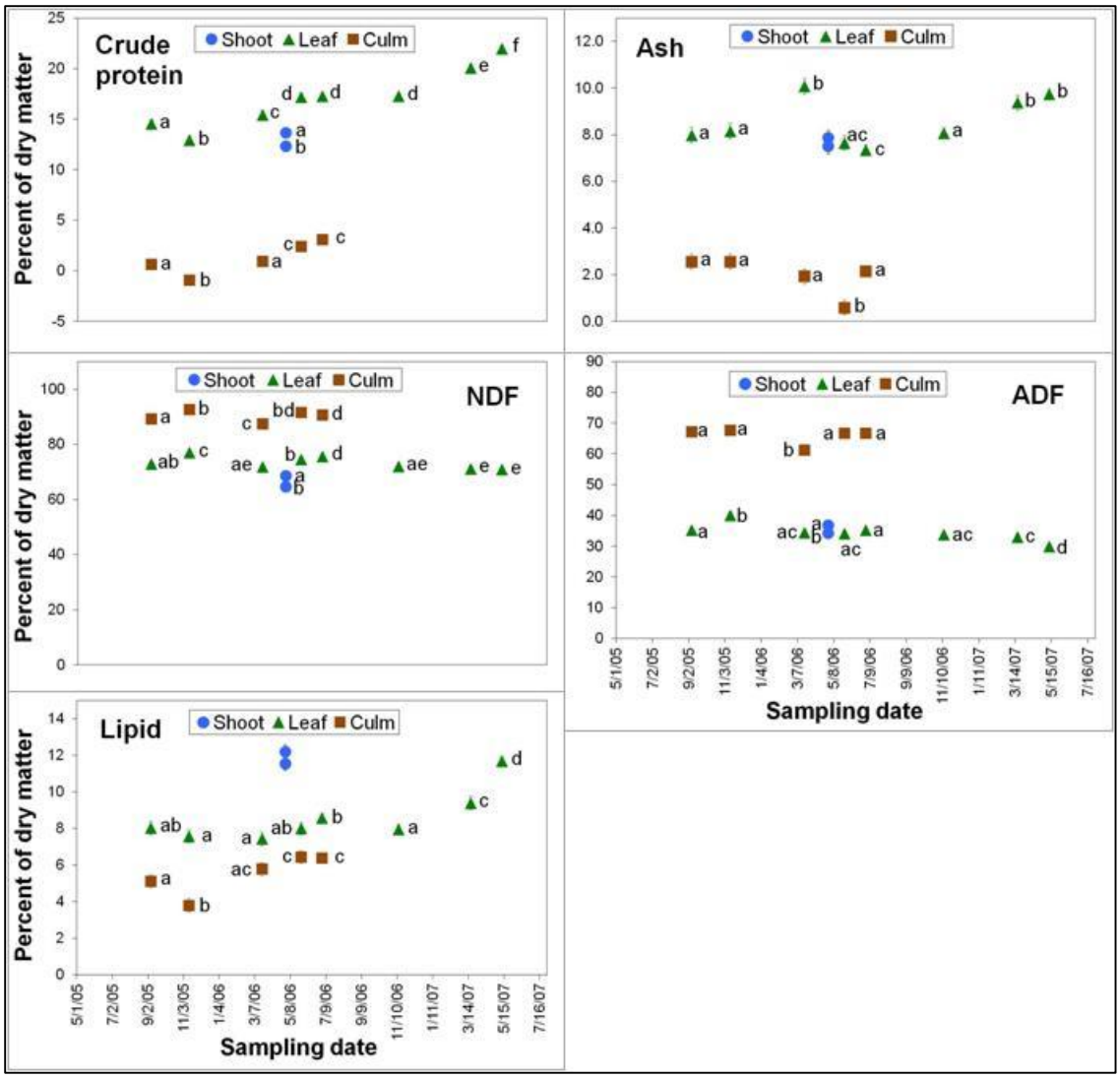

Figure 2.7 Nutrient concentration of bamboo by sampling date: *Phyllostachys rubromarginata*.

Bamboo was sampled from the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and May 2007. Least-square means are adjusted for effects of ramet age via mixed-model repeated-measures ANOVA (PROC MIXED; SAS Institute, 2012), separated by plant part, with subplot as the repeated unit. Means for shoots, leaves, and culm (central, woody stalk) are presented separately. Letters indicate within-part differences across stages of development ($P < 0.05$); bars indicate standard error.

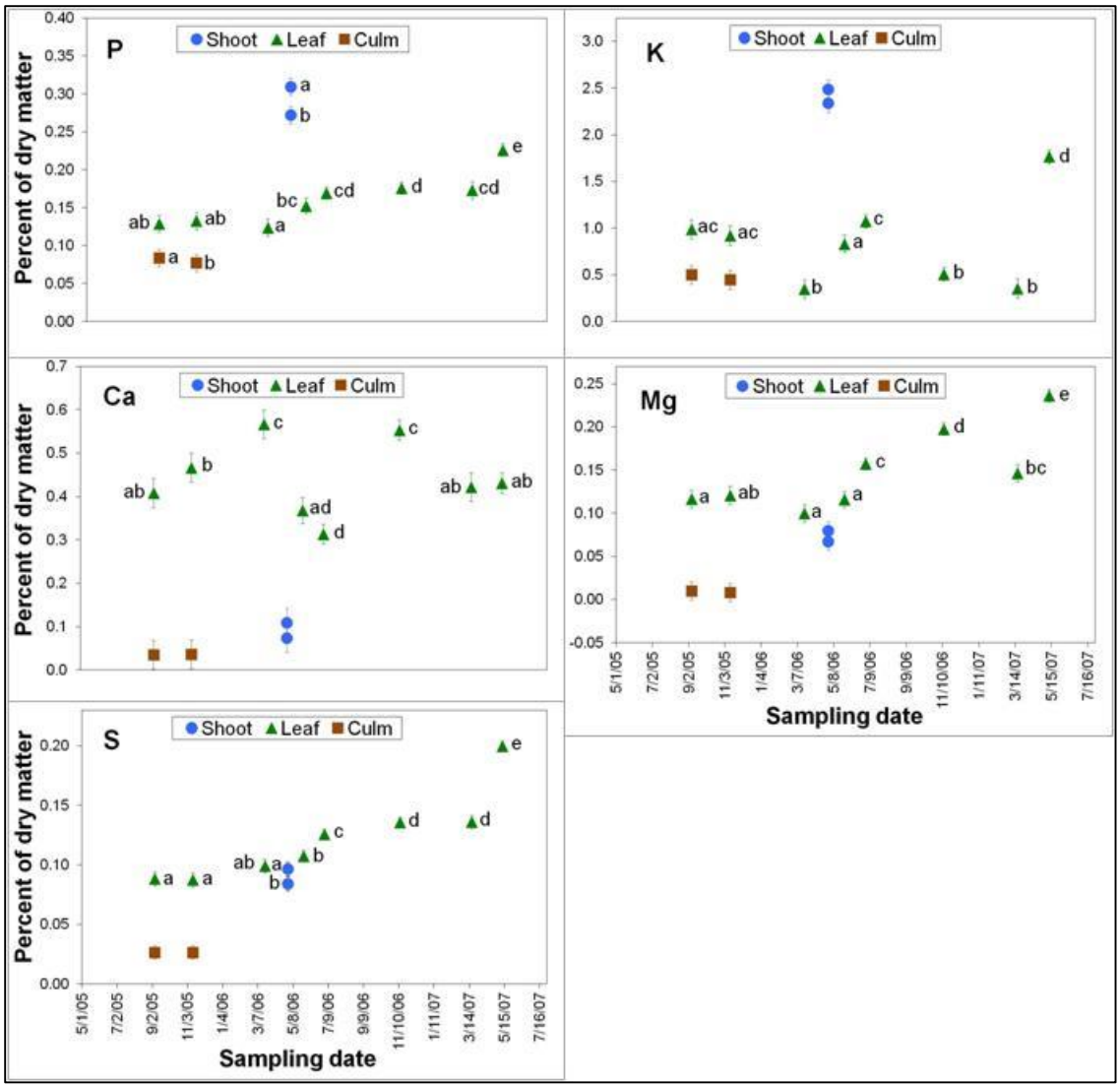

Figure 2.7 (Continued)

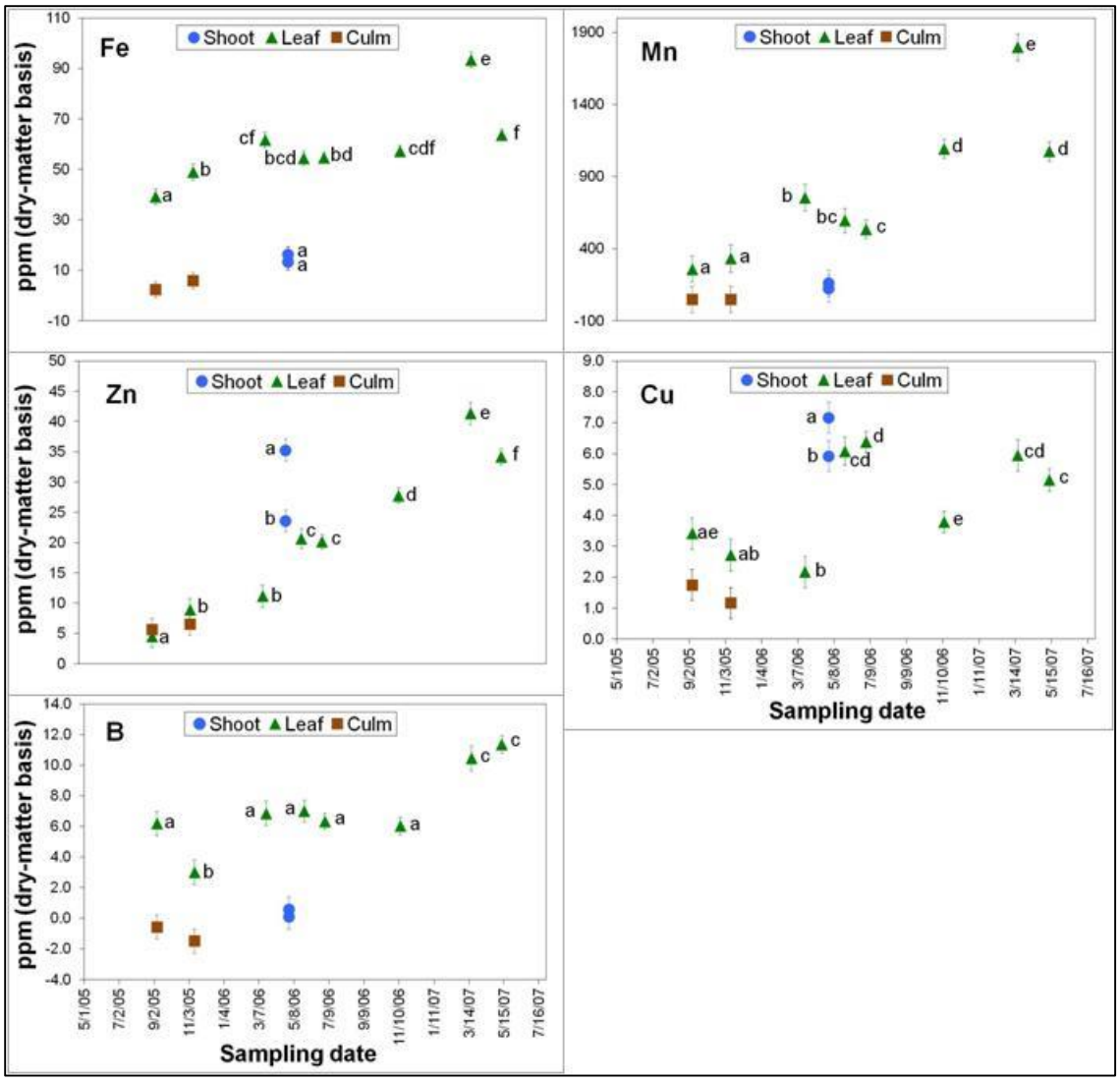

Figure 2.7 (Continued)

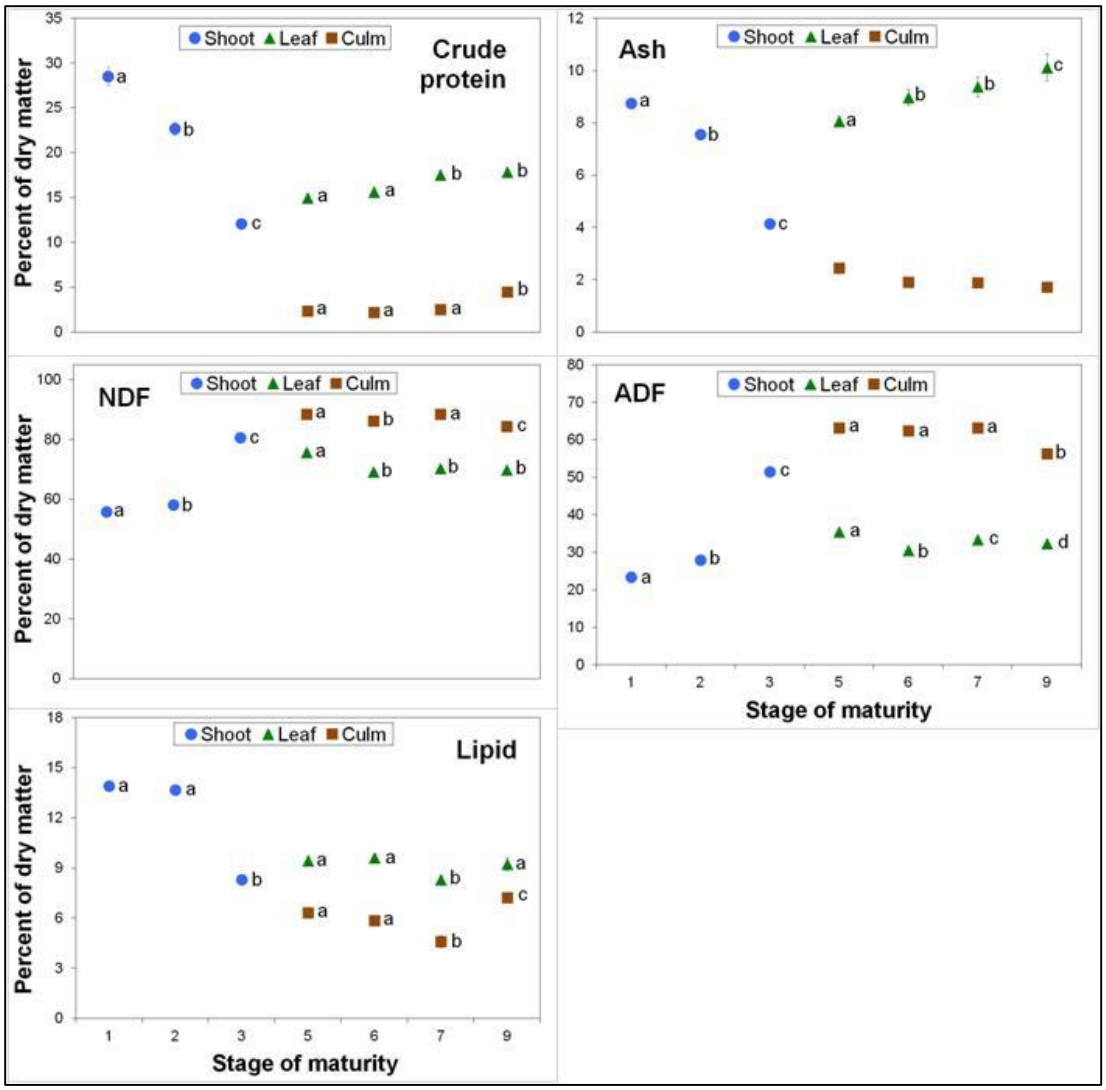

Figure 2.8 Nutrient concentration of bamboo by stage of maturity: *Phyllostachys aureosulcata*.

Data represent ramets < 1 year old. Stages of development are defined as follows: 1 = early shoot emergence (ramet 15 to 45 cm tall); 2 = later shoot emergence (ramet ~1 m tall); 3 = ramet elongation (maximum height has been reached, sheaths are shed, branches jointed); 5 = 30 days after leaf emergence; 6 = 90 days after leaf emergence; 7 = first freeze (mid-November); 9 = preparation for shoot emergence (March). Bamboo was sampled from the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and May 2007. Means are adjusted for study year via repeated-measures ANOVA (PROC GLM; SAS Institute, 2012), separated by plant part, with subplot as the repeated unit. Means for shoots, leaves, and culm (central, woody stalk) are presented separately. Letters indicate within-part differences across stages of development ($P < 0.05$); bars indicate standard error.

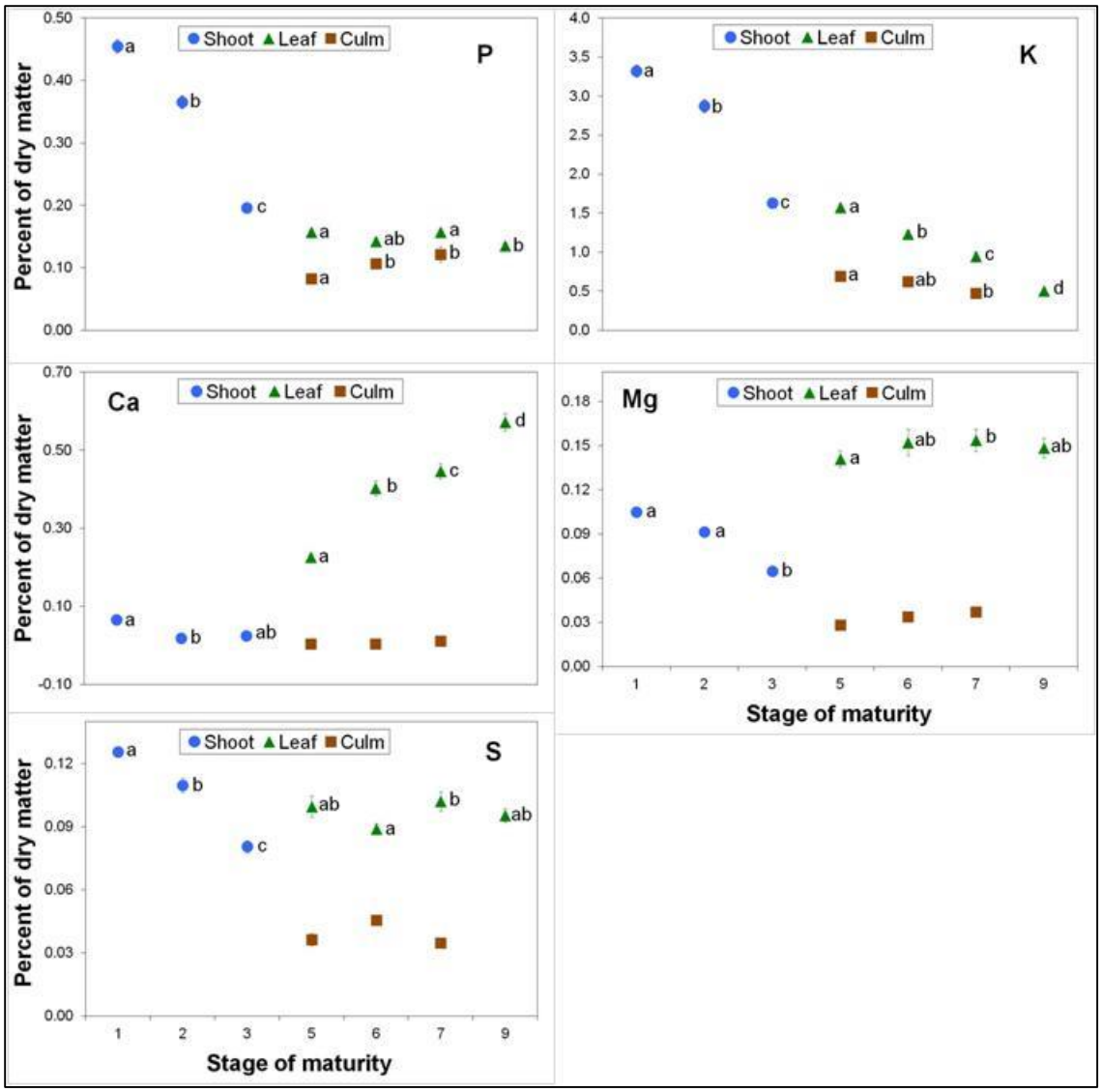

Figure 2.8 (Continued)

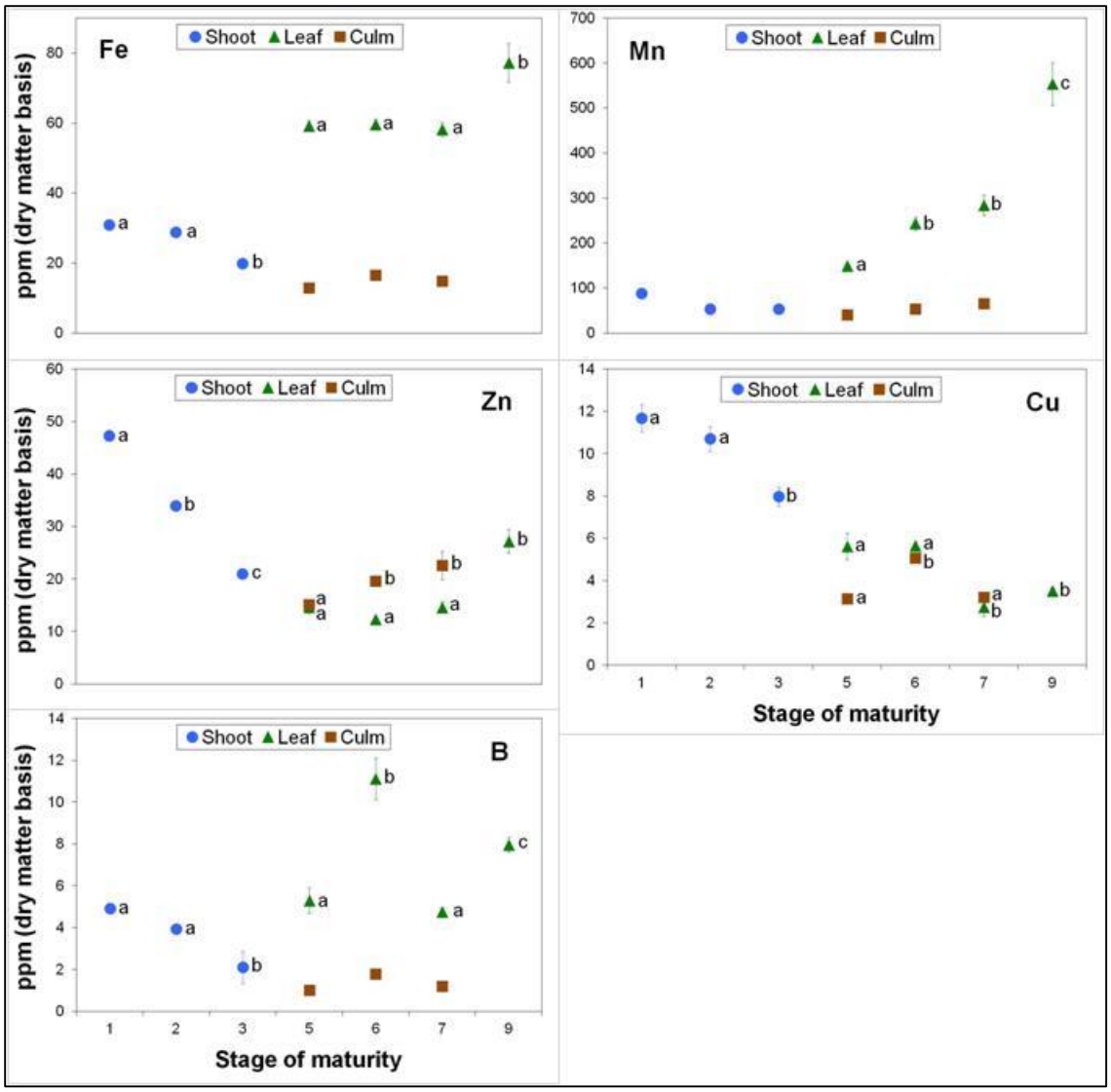

Figure 2.8 (Continued)

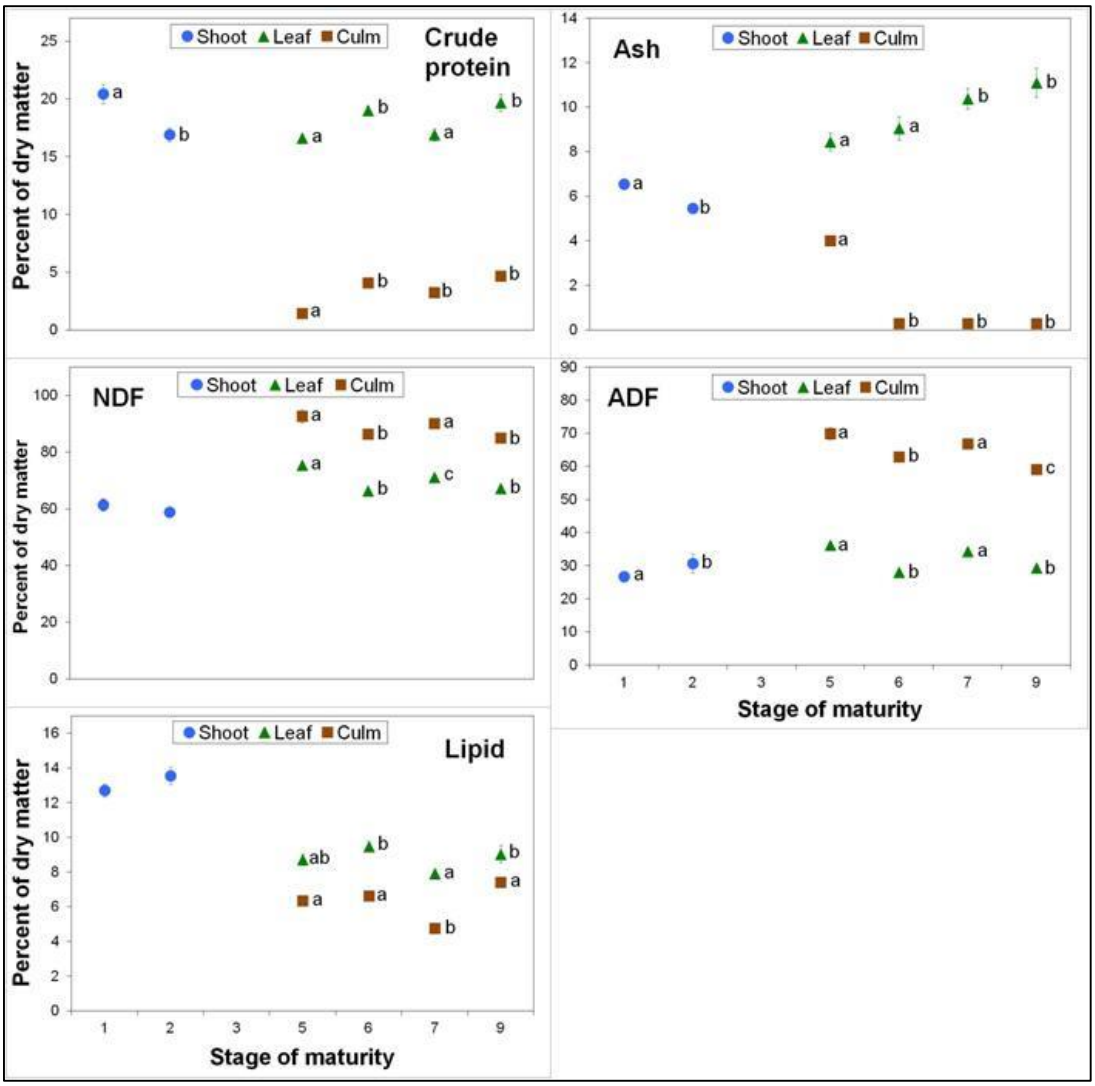

Figure 2.9 Nutrient concentration of bamboo by stage of maturity: *Phyllostachys glauca*.

Data represent ramets < 1 year old. Stages of development are defined as follows: 1 = early shoot emergence (ramet 15 to 45 cm tall); 2 = later shoot emergence (ramet ~1 m tall); 3 = ramet elongation (maximum height has been reached, sheaths are shed, branches jointed); 5 = 30 days after leaf emergence; 6 = 90 days after leaf emergence; 7 = first freeze (mid-November); 9 = preparation for shoot emergence (March). Bamboo was sampled from the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and May 2007. Means are adjusted for study year via repeated-measures ANOVA (PROC GLM; SAS Institute, 2012), separated by plant part, with subplot as the repeated unit. Means for shoots, leaves, and culm (central, woody stalk) are presented separately. Letters indicate within-part differences across stages of development ($P < 0.05$); bars indicate standard error.

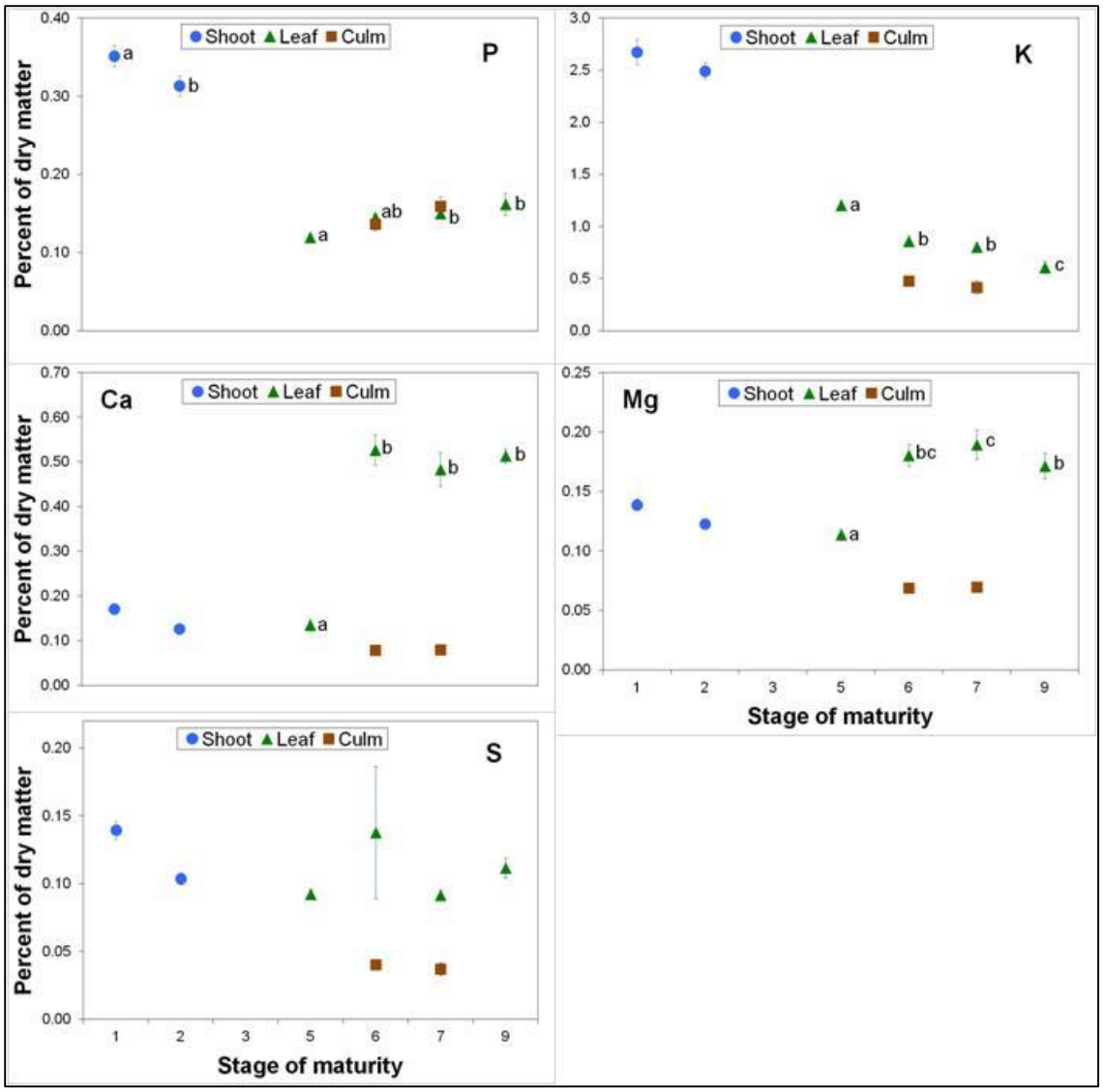

Figure 2.9 (Continued)

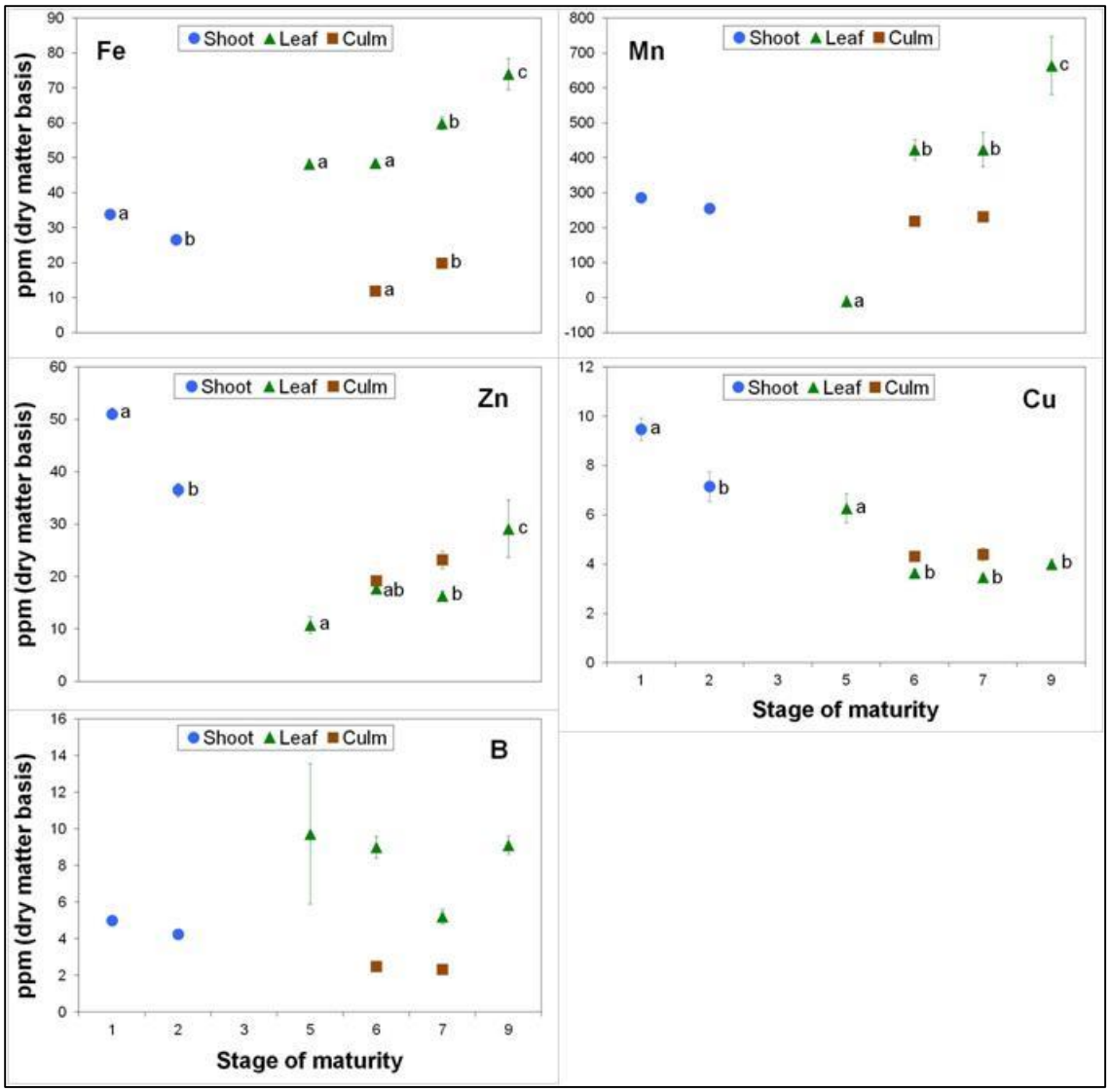

Figure 2.9 (Continued)

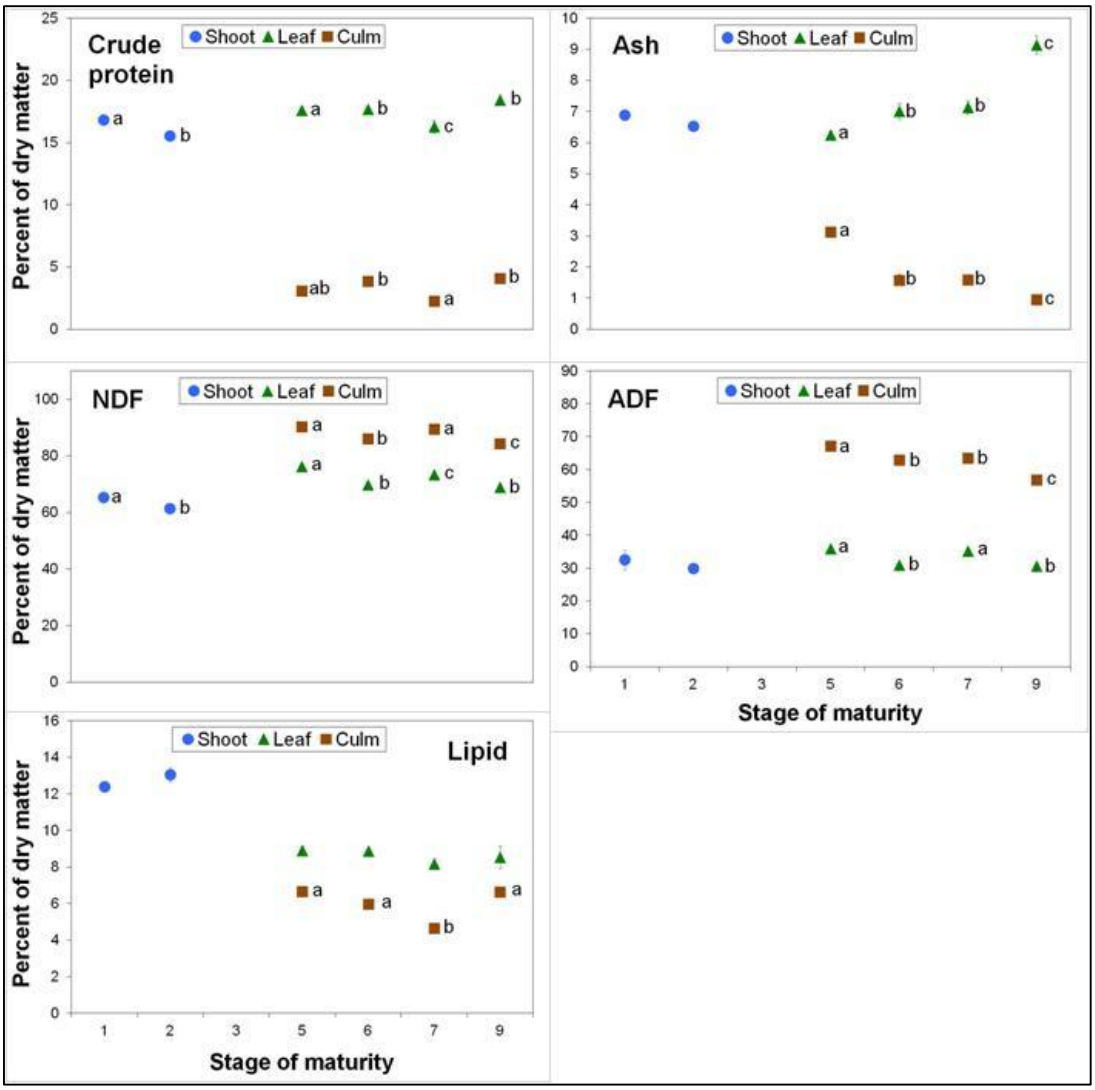

Figure 2.10 Nutrient concentration of bamboo by stage of maturity: *Phyllostachys rubromarginata*.

Data represent ramets < 1 year old. Stages of development are defined as follows: 1 = early shoot emergence (ramet 15 to 45 cm tall); 2 = later shoot emergence (ramet ~1 m tall); 3 = ramet elongation (maximum height has been reached, sheaths are shed, branches jointed); 5 = 30 days after leaf emergence; 6 = 90 days after leaf emergence; 7 = first freeze (mid-November); 9 = preparation for shoot emergence (March). Bamboo was sampled from the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and May 2007. Means are adjusted for study year via repeated-measures ANOVA (PROC GLM; SAS Institute, 2012), separated by plant part, with subplot as the repeated unit. Means for shoots, leaves, and culm (central, woody stalk) are presented separately. Letters indicate within-part differences across stages of development ($P < 0.05$); bars indicate standard error.

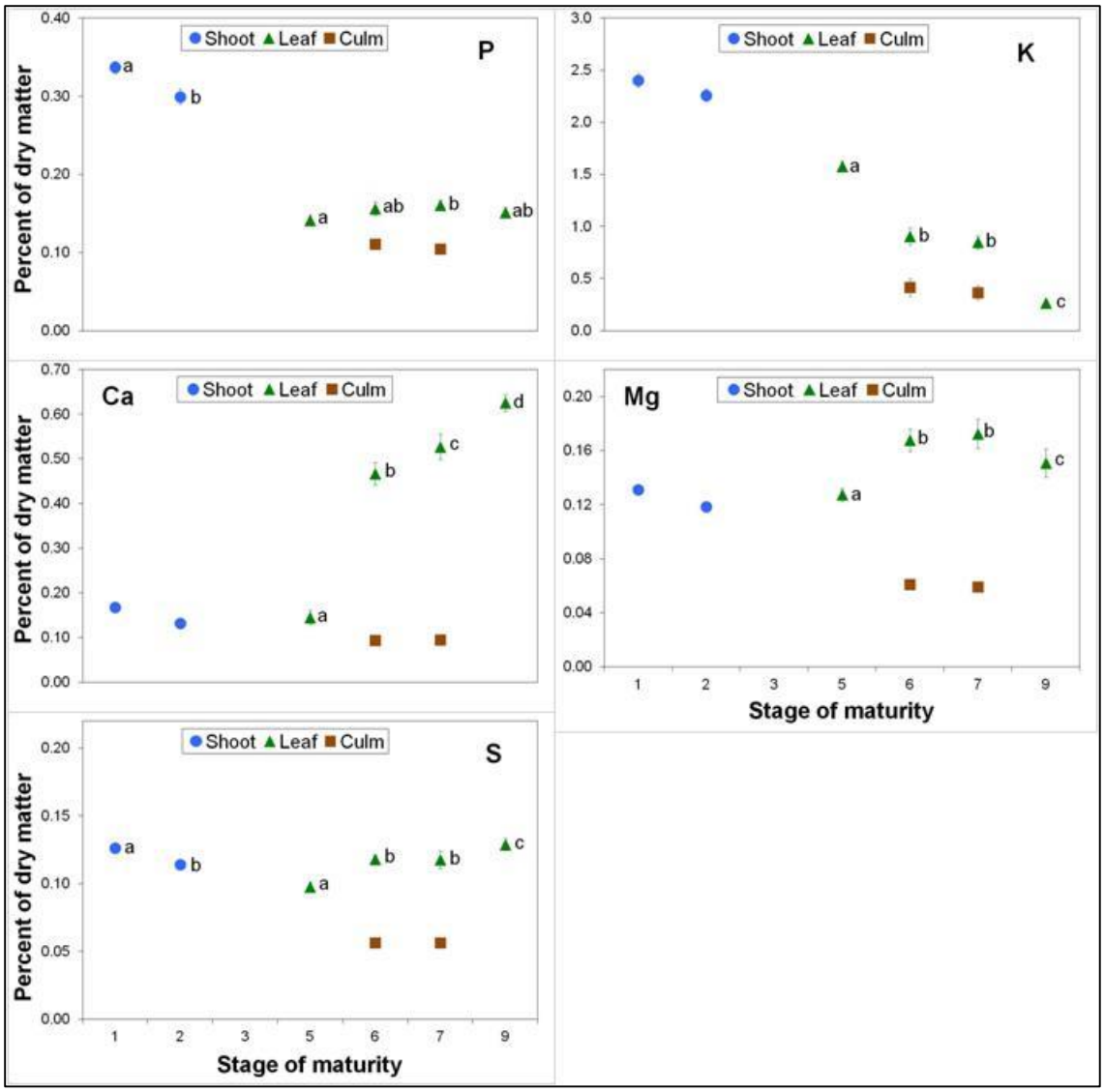

Figure 2.10 (Continued)

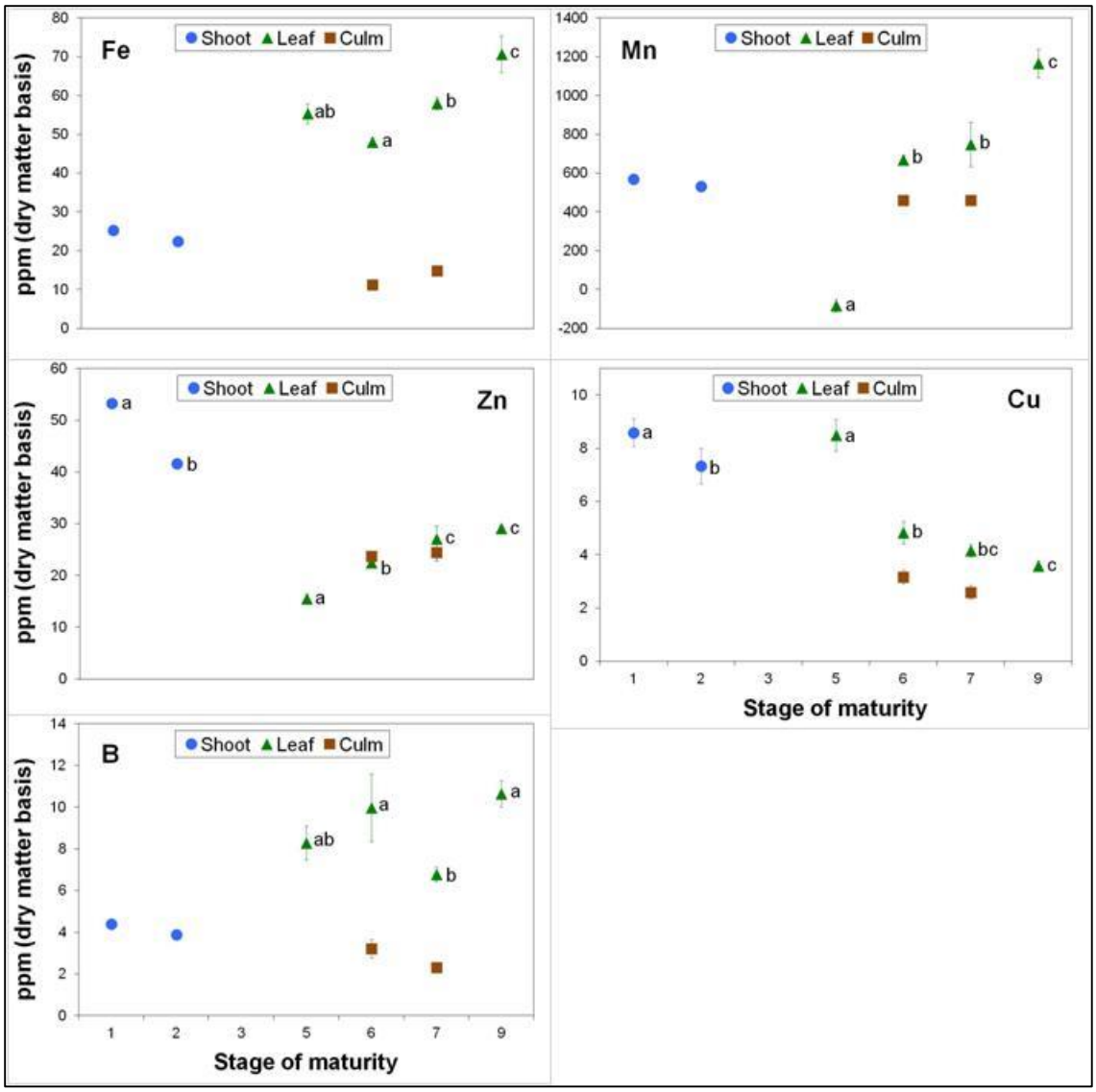

Figure 2.10 (Continued)

CHAPTER III

RECRUITMENT, MORTALITY, AND BIOMASS PRODUCTION OF *PHYLLOSTACHYS* BAMBOOS: TOWARD SUSTAINABLE ABOVEGROUND DISTURBANCE

Abstract

Responses of clonal plants to aboveground disturbance can be complex, depending on the intensity, timing, and nature of disturbance, and the degree of physiological integration among individual units (ramets) of a clonal organism (genet). Disturbance-induced interruption of intra-annual cycles of photoassimilate accumulation and storage can compromise genet-level recruitment and growth in subsequent seasons. This study sought to quantify bamboo-stand recruitment, mortality, and biomass production across multiple years, under varying intensity of aboveground disturbance. We established replicate enclosures within established monoculture stands of *Phyllostachys aureosulcata* (PLLAU), *P. glauca* (PLLGL), and *P. rubromarginata* (PLLRU), located at the Shelby County AgriCenter, Memphis Tennessee, USA. Over 3 years, we applied 3 disturbance treatments (control, 3% and 20% annual removal of biomass), and quantified parameters of production, stand maturity, recruitment and mortality: ramet height, basal diameter of culm (stem), height of lowest branch, dry ramet weight, and density of live and dead mature ramets and shoots. We detected disturbance effects on lowest-branch height for PLLGL, and on culm dry weight for PLLRU.

However, prescribed disturbance treatments were overshadowed by stochastic events in Year 2, including drought conditions and peak populations of roosting native blackbirds, resulting in significant bamboo defoliation. New ramets which followed were reduced in height, culm diameter, and biomass, although recruitment increased for PLLRU. These observations reflect clonal responses to photoassimilate restriction, and underscore the importance of canopy leaf area to subsequent primary production. Our findings are intended to inform bamboo-stand management for captive populations of primary consumers, in particular the giant panda.

Introduction

Bamboos, like all graminoids, are clonal species. Members of tribes Bambuseae (tropical woody bamboos) and Arundinarieae (temperate woody bamboos), in particular, display gregarious monocarpy, reproducing by sole means of vegetative propagation throughout the life of the clone until a single coordinated flowering event, immediately followed by death of the entire clonal unit (Schaller et al. 1985; Keeley and Bond 1999; Stern et al. 1999; Clark 2006). Exclusively vegetative propagation has a number of implications: (1) physical interconnection among asexually-produced offspring, (2) particular seasonal and interannual patterns of nutrient cycling, recruitment, and renewal of existing vegetation, and (3) complex effects of aboveground disturbance on remaining portions of the clone.

In vegetative propagation, genetically-identical daughter stems (ramets) arise from a parent plant through belowground runners (rhizomes). The maintenance of physical connections among ramets to form a collective (genet or clone) conveys certain advantages, among them the ability to act as a single functional organism. Physiological

integration allows for colony-level responses to stimuli through biochemical signaling (Stuefer et al. 2004), as well as sharing of resources and maximal exploitation of heterogeneous environments (Stuefer et al. 2002). The capacity for lateral rhizomatous extension also means that the genet is not stationary: it can expand its radius (sometimes selectively), allowing it to adapt to changes in resource availability through time or space by quickly projecting new growth into uncolonized soil (Piqueras et al. 1999).

Because of this reliance on belowground lateral expansion, clonal plants, particularly the woody bamboos, often exhibit a particular pattern of recruitment and therefore nutrient flux to support recruitment and growth. Reproduction commonly occurs in a burst of shoot production and rapid growth, usually in spring, just before the period of maximum sunlight intensity in early summer (Kleinhenz and Midmore 2001). Bamboo shoots elongate quite rapidly, sometimes growing from emergence to full height within a matter of days (Recht and Wetterwald 1996; this study). Shoot emergence for an entire stand is sometimes completed within 2 to 3 weeks; maximum shoot elongation, shedding of the outer sheath, and exposure of branches (called jointing) can occur within 1 to 2 weeks of shoot emergence (Recht and Wetterwald 1996; Kleinhenz and Midmore 2001; this study). A flush of leaf growth follows, with upregulation of photosynthetic enzyme systems through the length of summer. As available sunlight wanes in autumn and winter, leaves senesce but do not all die; only the oldest leaves are shed and the stand remains otherwise evergreen (Li et al. 1998 a,b; Kleinhenz and Midmore 2001).

Throughout this annual growth cycle, nutrient accumulation and flux follow suit. Clonal plants demonstrate a strong seasonal effect in particular on the amount of carbohydrate accumulation and storage, as well as the form of carbohydrate accretion

(sugars vs. starches; Zasada et al. 1994; Landhausser and Lieffers 1997, 2002; Li et al. 1998a). In clonal shrubs and trees, stored starches from the root system are mobilized in spring to support new growth, followed by an accumulation of sugars and proteins in the leaf canopy with increased photosynthetic capacity during the growing season. With the onset of autumn senescence, soluble sugars from aboveground organs are converted to stored starches in the rhizomes and roots (Zasada et al. 1994; Landhausser and Lieffers 1997, 2002). Because aboveground recruitment in clonal species depends on nutrient reserves in belowground structures, this cycle of nutrient shunting is important to the maintenance of the stand, and a linear quantitative relationship between root stores and new shoots or suckers has been shown in multiple species (Zasada et al. 1994, Landhausser and Lieffers 1997, 2002).

Carbohydrate and nutrient dynamics in Arundinarieae seem to follow along the same lines as those of other woody clonal species (Li et al. 1998a). In addition, members of this tribe demonstrate particular cyclicity in leaf turnover. Individual leaves normally have a lifespan of 2 years, and are shed late in their second winter, just before shooting (Kleinhenz and Midmore 2001). The period of maximal photosynthetic capacity occurs during the first year, with more nonstructural carbohydrates and other nutrients present than in second-year leaves (Li et al. 1998a). Thus, leaf-age structure becomes particularly important: in a stand that is balanced with respect to 1-year-old versus 2-year-old leaves, year-to-year photoassimilate production remains relatively stable – typical of mature, established stands. In younger stands, all leaves may be of the same age, and may experience a multi-annual cycle of leaf shedding, leaf density, and average

leaf maturity (Li et al. 1998 a,b), and consequently rates of carbon fixation may be more heterogeneous among years.

Aboveground disturbance in clonal species such as bamboo can cause structural changes in individual stems or an entire clonal unit. Many herbaceous species respond to moderate clipping or grazing through compensatory growth and an increase in new stem density, with a net increase in biomass (McNaughton 1983, 1984, Herms and Mattson 1992, Wilsey 2002). Structure and growth parameters of clonal trees, on the other hand, tend to respond negatively to herbivore-induced disturbance (Romme et al. 1995, Reichenbacker et al 1996, Zeigenfuss et al. 2002), with mixed responses to other aboveground alterations such as fire (Romme et al. 1995). Some clonal shrubs respond in the same manner as herbaceous vegetation, with a rapid increase in stem density and new rhizomes following disturbance in *Rubus spectabilis* (Zasada et al. 1994), and an increase in bud production rate of *Salix arctica* grazed by muskoxen (Tolvanen et al. 2002).

Evidence from bamboos is equivocal. The neotropical woody bamboo *Otatea acuminata* responds to harvest with compensatory growth, and harvested sites showed reduced mortality and greater densities of mature ramets, a key predictor for the production of juvenile ramets (Vazquez-Lopez et al. 2004). Numbers of healthy ramets were enhanced by increasing harvest intensity (Vazquez-Lopez et al. 2004). A recently-harvested stand of *Dendrocalamus strictus* in a dry tropical forest showed reduced aboveground biomass and overall reduced total net productivity as opposed to a more mature stand, with greater belowground production as a percent of total production after harvest (Tripathi and Singh 1994). *Bambusa bambos* in the same region showed a progressive increase in aboveground biomass with plantation age until year 6, after which

the trend was reversed (Shanmughavel and Francis 1996, 2001). In a 2-year study of giant panda-induced disturbance on *Fargesia qinlingensis*, Wang et al. (2007) found static ramet populations in year one but an increase in recruitment relative to mortality in year two, with an overall decrease in ramet density over both years. Such complexities may reflect a normal year-to-year cycle in leaf density per ramet (Li et al. 1998a, b), which dictates yields of photosynthetic assimilates and causes cyclical variation in shoot emergence and survival (Taylor and Qin 1993). This cycle may also obscure predictions of bamboo clonal dynamics under disturbance.

The phenomenon of rapid shooting and elongation of multiple ramets within a few weeks' time places particular demands on belowground nutrient stores for bamboos. Because the season of active shoot growth corresponds with a time when senescence occurs in the oldest leaves, photosynthetic capacity is reduced and new ramets must rely even more on stored nutrients for growth (Li et al. 1998a). Aboveground disturbance in temperate bamboos can interrupt normal cycles of nutrient availability, potentially altering recruitment rates, canopy leaf area, and photosynthetic capacity. In mature stands that are balanced with respect to new vs. old leaves, and therefore do not undergo annual oscillations in average leaf maturity (Li et al. 1998b), catastrophic disturbance could catalyze the large cyclical variances in new leaf production typical of much younger stands.

A number of threatened or endangered species depend on bamboo as a primary food source, or as a significant component of the diet. These include the red panda (*Ailurus fulgens*) (Bleijenberg and Nijboer 1989), bamboo lemurs (*Hapalemur* spp.; Tan 1999), and the mountain gorilla (*Gorilla beringei*; Rothman et al. 2007). Perhaps the

most famous primary consumer of bamboo, however, is the giant panda (*Ailuropoda melanoleuca* David; Chorn and Hoffman 1978), a specialist herbivore whose diet consists almost exclusively of Arundinarieae (99% or more of the diet; Schaller et al. 1985; Edwards et al. 2006). Despite numerous adaptations of the skeletal structure for processing such a feedstuff (e.g., broad, large molars, thickened tooth enamel, enlarged muscular attachments on the skull, and the famous modified radial sesamoid or "pseudothumb"), the giant panda possesses no adaptations of the digestive tract to assist with fiber digestion (Schaller et al. 1985; Edwards et al. 2006). Consequently, its digestive efficiency is among the least of all land mammals (10 to 40% on a bamboo-only diet; Schaller et al. 1985; Long et al. 2004; Edwards et al. 2006; Sims et al. 2007), and pandas need to maintain extreme rates of dry-matter intake to meet energetic and nutritional demands (MZS 2006; Sims et al. 2007).

The giant panda does face direct threats to survival in the form of poaching or by-catch in snares set for other species (Schaller et al. 1985). However, like many other endangered and threatened species, a greater problem is the pervasive influence of habitat disturbance. The historic range of the species, which once included much of China, has been progressively reduced to smaller areas at higher elevations as bamboo forests have been turned into agricultural lands. The government of China has made significant strides to control human settlement in wildlife reserves and to reduce the rate of deforestation, however clearing of land for crops or logging of the forest for firewood or raw materials does still occur (WWF 2004). Thus, bamboo in panda habitat is subject not only to background rates of disturbance from animal foraging, but also to more pervasive and unpredictable anthropogenic disturbances (Schaller et al. 1985).

We undertook the present study in an effort to elucidate effects of aboveground disturbance on temperate bamboo-stand stability and biomass production. We sought to examine factors affecting bamboo-stand production across multiple years, under varying disturbance intensites. Our goal was to provide information on maximum tolerable disturbance intensity, as well as recommended sustainable rates of bamboo harvest.

Materials and methods

Research site

We conducted a 3-year investigation (June 2005 to June 2008), within a 4-ha plot of land (35° 7'57"N, 89°49'49"W) at Shelby County AgriCenter in Memphis, Tennessee, USA (Fig. 3.1). The site, a former cotton field, was established by the Memphis Zoo (MZ) in 2001, for the purpose of growing bamboo to feed giant pandas. Commercially-cultivated bamboo from 7 species was bought from local nurseries and planted in 2001 and 2002, in clumps of 2 to 5 ramets, spaced 0.5 to 1 m apart, to establish 0.4-ha monoculture plots maintained in 10 rows per plot. At the initiation of the study, aisles between rows had historically been maintained by MZ personnel, by periodic mowing and use of glyphosate herbicide. After initiation of the study, mowing within experimental enclosures was suspended. This location is characterized by sandy loam soils, bordered by manmade ponds to the west and south, a 2-lane local-access road to the north, and agricultural fields (historically cotton) to the east and just across the northern road.

Study species

The bamboo species selected for this study all belong to genus *Phyllostachys*, one of the largest and most widespread genera of woody bamboos (Renvoize and Hodkinson 1997; Kleinhenz and Midmore 2001). Bamboos of this genus are easily cultivated, commercially available, and grow well in many locations all over the world. For that reason, many zoos rely on *Phyllostachys* spp. as their staple forage for species such as giant pandas (Edwards et al. 2006). *Phyllostachys* spp. are monopodial bamboos, with leptomorphic ("running") rhizome systems (Kleinhenz and Midmore 2001). Primary shoot production occurs in spring (April to May at this location), with an occasional secondary shoot crop in autumn (August or September), depending on local conditions in a given year. We focused on 3 species for this study, due to their popularity as a staple forage for giant pandas at MZ and other zoological institutions (MZS 2006; Edwards et al. 2006, Sims et al. 2007): *Phyllostachys aureosulcata* (PLLAU)*, P. glauca* (PLLGL)*, and P. rubromarginata* (PLLRU). The material originally planted in each of these plots was of differing genet age, such that each species also represents a different stage of whole-stand maturity: PLLGL was a mature stand, with greater ramet heights than any other species at the site and the least ramet density; PLLAU was a young, shorter, dense stand undergoing marked year-to-year increases in stand height; and PLLRU was at a stage of maturity intermediate to PLLGL and PLLAU (Table 3.1).

Experimental design

Within each of the 3 species plots under study, we established 4 replicated enclosures (approximately 24 x 15 m each), such that equal bamboo density within enclosures was optimized. A sampling grid was established, and each enclosure was

divided into three 6 x 9-m subplots with a 3-m buffer around the edge of the enclosure, within which each of 3 experimental disturbance treatments were assigned to subplots randomly: control (no bamboo removal), 3%/year removal of individual live ramets, and 20%/year removal (Fig. 3.2). Disturbance intensities were selected to simulate (1) "natural" disturbance, based on typical grazing rates by wild giant pandas (3% removal; Wang et al. 2007), and (2) common rates of anthropogenic disturbance, based on harvest rates often employed by zoos feeding giant pandas (20%; MZS 2006).

At study initiation, at least 50 live ramets per subplot were randomly pre-identified for later sampling (located evenly throughout each subplot), and tagged to prevent removal during application of disturbance treatments. Ramet removal for treatment effects occurred at quarterly intervals (January, April, July, October), with live ramets removed in a uniform manner throughout the stand. Every autumn (September or October), live ramet densities were quantified at four locations within each subplot, and used to estimate total live ramet density per subplot, from which biomass removal rates were calculated for the subsequent 4 quarters. A fertility regime was applied at the initiation of the study (7 June 2005), and each autumn (October) and winter (January or February), at least 1 month prior to subsequent sampling. Soil was sampled in September from 4 uniformly-spaced locations per replicate enclosure, pooled by bamboo species, and fertilizer was applied (Table 3.2) according to recommendations for temperate grasses by the Mississippi State University Cooperative Extension Service (MCES) Soil Testing Laboratory. Maximum canopy height was recorded within each enclosure after elongation and leafing of the year's shoot crop (July to September).

Sampling

Sampling of bamboo was intended to occur at 9 times per year for each bamboo species, at points throughout the year corresponding to significant developmental stages of bamboo growth and maturation: 1 = early shoot emergence (ramet 15 to 45 cm tall); 2 = later shoot emergence (ramet ~1 m tall); 3 = ramet elongation (maximum height has been reached, sheaths are shed, branches jointed); 4 = leaf emergence; 5 = 30 days after leaf emergence; 6 = 90 days after leaf emergence; 7 = first freeze (mid-November); 8 = mid-winter (January); 9 = preparation for shoot emergence (March). Once sampling began, it became evident that stages 3 and 4 were difficult to distinguish, and so stage 4 sampling was eliminated, leaving 8 sampling points per year. All sampling occurred within 2 m of the eastern edge of historic mowed aisles, to control for variation in peak sun angle. In Year 1, 1 ramet per treatment per enclosure was clipped and removed (12 samples per developmental stage per species). For stages 1 and 2, an additional 3 and 1 ramets (respectively) were removed and pooled by subplot, to provide adequate sample mass for later nutritional analyses (published elsewhere). As each year's shoot crop reached stage 6 (August to September), at least 40 ramets < 1 year old were located within 0.5 m of previously-tagged ramets, and themselves tagged with a different color, to allow for comparisons among age classes in subsequent years. Thus, in Year 2, at each sampling point, 1 ramet > 1 year old and a paired ramet < 1 year old was sampled (24 total samples per developmental stage per bamboo species), and in Year 3, 1 ramet > 2 years old, 1 ramet > 1 year old, and 1 ramet < 1 year old were sampled (36 samples per stage per bamboo species).

Sampling proceeded by randomly identifying a focal ramet from among those tagged at study initiation. A 1 x 1-m quadrat was placed with the focal ramet at the center, and all ramets within the quadrat were counted and classified as one of the following: live mature ramet (ramets at developmental stage 5 or beyond), dead mature ramet, live shoot (ramets at stages 1 through 3), or dead shoot. After July of each year, dead shoots were no longer counted, as they had begun to decay by that point in time. After quantifying all vegetation, the focal ramet was cut at the base (point of contact with the soil, or just above the point of lateral rhizome branching), as well as the closest tagged ramet < 1 year old (if Year 2 of sampling), and the closest tagged ramet > 1 year old (if Year 3). All parameters measured for the focal ramet were also ascribed to the paired younger ramets sampled simultaneously. Location of the focal ramet was recorded with respect to the sampling grid, as well as distance to the edge of the bamboo row.

Cut ramets were bagged and transported on ice to Mississippi State University (MSU) North Farm Complex for processing. We measured each ramet's total height, the height of the bottom-most branch (an indication of bamboo-stand maturity), and the diameter of the culm (central, woody stem) within 5 cm of the cut base. Ramets from stages 5 through 9 were hosed to remove surface contaminants (dirt, bird feces, etc.), air-dried under refrigeration for 2 to 10 hours, and separated into leaf, branch, and culm (Fig. 3.3), again for later nutritional analyses. Ramets from stages 1 through 3 were kept intact. All samples were dried to constant mass at 60° C. Sample weights were recorded (1) prior to separation into various plant parts, (2) just prior to placement in drying ovens, and (3) after removal from drying ovens and cooling to room temperature.

Statistical analyses

In order to test for factors that may affect biomass production, we performed a residual analysis, in which we first calculated stem volume as a mathematical index of expected biomass Fang et al. 1998):

$$\text{Stem volume} = (\text{Ramet height in cm}) \times (\text{Basal culm diameter in mm}) \qquad (3.1)$$

We then regressed measured biomass (dry weight in kg) on calculated stem volume (PROC REG; SAS Institute 2012), and determined the residual variation for each ramet, or the degree to which actual biomass deviated from mean expected biomass. This new variable, which we termed residual biomass, was included in subsequent analyses along with directly-observed variables. We also wished to quantify live versus dead ramets not only by count but by proportion, and therefore calculated arcsine-transformed percent of total ramets for the following: live mature ramets, live shoots, dead mature ramets, dead shoots, and total dead ramets.

Analyses of stand production and maturity parameters (residual biomass, ramet height, bottom branch height, basal culm diameter, ramet dry mass, and dry masses of leaf, branch, and culm components) were conducted via a series of repeated-measures Analyses of Variance. Because of substantial differences in origin of ramets, planting history, and stand maturity among PLLAU, PLLGL, and PLLRU, bamboo species were analyzed separately. Changes through time were analyzed in a 2-way design, with subplot as the repeated unit, testing for main effects and interaction of sampling date and ramet cohort (year of emergence as a shoot). Because sampling date was a random effect, these analyses were performed in a mixed model (PROC MIXED; SAS Institute

2012), using Satterthwaite approximation for effective degrees of freedom. Effects of aboveground disturbance treatments were analyzed in a split-plot repeated-measures design (PROC MIXED), with replicate enclosure as the repeated unit, sampling date as the main-plot factor, and disturbance treatment as the subplot factor, with ramet cohort as an additional main-plot effect.

In addition to the indicators of stand production just described, we also performed repeated-measures ANOVAs of (1) live mature ramets per m^2, and (2) arcsine-transformed percent live mature ramets. However, because measures of ramet density were the same for all sampled ramets within a given 1-m^2 quadrat, we performed a 1-way repeated-measures ANOVA only, again with subplot as the repeated unit, testing for the main effect of sampling date (PROC MIXED).

Measures of bamboo-stand recruitment and mortality were analyzed in a simple 2-way ANOVA, testing for main effects of disturbance treatment and study year. A general linear model was used (PROC GLM; SAS Institute 2012), as all main effects were fixed. Indicators of recruitment (live shoots, live mature ramets, and the corresponding arcsine-transformed percents) were quantified at Sampling Period 3 (ramet elongation and jointing), at which time all shoots have emerged. Indicators of mortality (dead shoots, dead mature ramets, total dead ramets, and the corresponding arcsine-transformed percents) were quantified at Sampling Period 5 (30 days after leaf emergence), when all shoot mortality has occurred, but dead shoots have not yet decomposed.

Monthly weather parameters for the study site were obtained from the U.S. National Oceanic and Atmospheric Administration (NOAA), taken at an observation post

located at the Shelby County AgriCenter (35° 7'47"N, 89°48'13"W), 2.5 km from our study site (Table 3.3, Fig. 3.4). To test for potential covariates, we performed correlations (PROC CORR; SAS Institute 2012) between response variables and (1) mean monthly temperature, and (2) total monthly precipitation. For variables with significant correlations, we then tested for homogeneity of the slope of the covariate relationship (PROC GLM, with sampling date as a random effect), before performing Analyses of Covariance. For all analyses described herein, a significance level of $\alpha \leq 0.05$ was used.

Results

In winter 2007, a portion of the bamboo in enclosures C and D of our PLLAU study plots was accidentally removed for animal forage; thus, these two enclosures were excluded from the final 2 sampling periods for that species. Otherwise, our dataset was balanced for the first 2 years of sampling and for the entire study period for PLLGL and PLLRU.

Biomass production and stand maturity

Disturbance

For PLLRU, dry branch weight ($F_{2,308} = 3.71$, $P = 0.03$) and dry culm weight ($F_{2,350} = 3.02$, $P = 0.05$) were greater for ramets from 3%-removal subplots than for those from either control or 20%-removal subplots (Table 3.4). Otherwise, we did not detect disturbance effects on other measures of production and stand maturity ($P > 0.16$).

Temporal effects

For PLLAU, we detected an interaction between sampling date and ramet cohort ($P < 0.02$) for all production and maturity variables measured: residual biomass, ramet height, bottom branch height, basal culm diameter, and dry mass of leaves, branches, culm, and total ramets (Table 3.5). For PLLGL, we detected the same interaction ($P < 0.001$) for all variables but two: we found a main effect of sampling date ($P < 0.001$) and a strong tendency toward ramet cohort effects ($P = 0.054$) on mean dry weight of leaves, and we found a tendency toward sampling-date effects ($P = 0.08$) and a main effect of cohort ($P = 0.01$) on mean dry weight of branches (Table 3.6). For PLLRU, sampling date x ramet cohort interactions existed ($P < 0.001$) for all variables but mean dry weight of branches, for which we detected main effects of both sampling date ($P < 0.001$) and ramet cohort ($P < 0.001$;Table 3.7).

For all 3 species, ramet height was less for ramets that emerged as shoots in 2005 and 2007, as were bottom branch height and basal culm diameter; ramets that emerged in 2006 had the greatest values of all of these measures (Tables 3.5, 3.6, 3.7; Figs. 3.6, 3.7, 3.8,). Culm dry mass was the least for 2007 ramets (Tables 3.5, 3.6, 3.7; Fig. 3.12). For PLLAU, residual biomass was the least for ramets that emerged in 2007 (Table 3.5; Fig. 3.5). For PLLRU, residual biomass was the least for 2006 and 2007 ramets (Table 3.7; Fig. 3.5), and for PLLGL, 2006 ramets had the least residual biomass (Table 3.6; Fig. 3.5). For PLLAU, total ramet dry mass was greatest for 2006 ramets and least for 2007 ramets (Table 3.5; Fig. 3.9). For PLLGL and PLLRU, ramet dry mass was least for 2007 ramets (Tables 3.6, 3.7; Fig. 3.9). For all 3 species, branch dry mass was generally least for 2007 ramets (Tables 3.5, 3.6, 3.7; Fig. 3.11).

One-way ANOVAs showed sampling-date effects ($P < 0.001$), for live mature ramets and arcsine-transformed percent live mature ramets in all 3 bamboo species (Tables 3.8, 3.9, 3.10; Figs. 3.13, 3.14). For all cohorts and species, leaf dry mass decreased ($P < 0.001$) between October 2006 and April 2007 (Tables 3.8, 3.9, 3.10; Fig. 3.10).

Analyses of covariance

Mean monthly temperature correlated ($P < 0.05$) with ramet height, bottom branch height, basal culm diameter, arcsine-transformed percent live mature ramets, leaf dry mass, and ramet dry mass (Table 3.11). Total monthly precipitation correlated ($P < 0.04$) with residual biomass, ramet height, basal culm diameter, arcsine-transformed percent live mature ramets, branch dry mass, and ramet dry mass (Table 3.11). However, for none of these relationships was the slope of the covariate relationship homogeneous ($P < 0.001$), and ANCOVA analysis was not performed.

Recruitment and mortality

For PLLAU, later study years had smaller ($P < 0.01$) proportions of live shoots, greater absolute densities of live ($P = 0.03$) and dead ($P = 0.01$) mature ramets, a tendency ($P = 0.07$) toward greater proportions of dead mature ramets, greater ($P = 0.01$) densitites of total dead ramets, and greater ($P = 0.03$) proportions of total dead ramets, (Table 3.12). We did not detect disturbance effects ($P > 0.11$) on any variables measured for this species.

For PLLGL, later study years had smaller ($P < 0.001$) proportions of live mature ramets, greater ($P < 0.001$) absolute and proportionate densities of dead mature ramets,

and greater ($P < 0.001$) absolute and proportionate densitites of total dead ramets (Table 3.12). There was a tendency ($P = 0.07$) toward greater proportions of dead mature ramets in 3%-annual-removal subplots than either of the other 2 disturbance treatments (Table 3.12).

For PLLRU, greater densities of live shoots ($P < 0.001$) and live mature ramets ($P < 0.01$) were found in Year 2 compared to Years 1 or 3, but Year 3 had the smallest proportions of live shoots and generally less proportionate live mature ramets (Table 3.12). Year 3 had greater ($P < 0.001$) densities of dead mature ramets and total dead ramets, as well as relative proportions of the same (Table 3.12). 3%-annual-removal subplots tended to have the least densities of live mature ramets, both in absolute counts ($P = 0.07$) and proportions of total ramets present ($P = 0.08$; Table 3.12). For proportionate density of live shoots, study year and disturbance interacted ($P = 0.04$), such that 20%-removal subplots had fewer percent live shoots in Year 1 only than the other 2 treatments, and Year 3 had fewer percent live shoots than Year 1 for control and 3%-removal subplots (Table 3.12).

Discussion

Within Arundinarieae, bamboo-stand structure changes in very predictable ways as the stand grows and matures. Young clones are characterized by short, thin ramets, with closely-spaced branches extending all the way from the base to the apex, and very high ramet density (Kleinhenz and Midmore 2001). Each year's shoot crop is taller, with greater culm diameters, thicker culm walls and a greater degree of culm lignification (Kleinhenz and Midmore 2001; Wang et al. 2006). A progressive increase in height of the lowest branch is often seen, as basal branches develop, but then senesce and abscise

soon after jointing (J. Parsons, personal observation). At the same time, large-scale changes to ramet density typically occur. In the first few years, a large degree of new-shoot recruitment coupled with little mortality of older ramets leads to progressive increases in density, until a critical stage of maximum density is reached when older ramets are completely overtopped by newer growth. Radical senescence of the oldest ramets follows, with density of live ramets decreasing with colony age until a state of stable density and culm diameter is reached (Kleinhenz and Midmore 2001). Density of new shoots also decreases, with progressively suppressed recruitment in relation to clone age, until stability is reached and rhizome buds form only to replace individual ramets lost through sporadic (natural or stochastic) mortality (Kleinhenz and Midmore 2001).

Two processes exist which may explain these patterns of growth: classical competitive interactions, and intraclonal regulation. Evidence of both is seen in bamboos. Resource competition certainly explains many of the observed changes, particularly the phenomenon of successively taller ramets, as overtopping is used as a means of securing access to sunlight (Gurevitch et al. 2002). Changes in culm diameter and height of lowest branch follow as a natural result: culms must be broader and sturdier to support taller ramets, and basal branches become extraneous, since they will only be overshaded by more apical branches, and thus will serve no useful purpose in generation of photosynthates. They are shed to save resources that would be necessary for their maintenance. Competition may also explain patterns in ramet density, through the well-known process of density-dependent mortality or self-thinning (e.g., "–3/2 rule"; Gurevitch et al. 2002). Within-clone thinning is seen in other woody species (e.g., *Populus*), possibly due to the greater heights possible in woody clonals, or more likely

the result of weak clonal integration (Peltzer 2002) – as opposed to herbaceous clonal species, which rarely exhibit self-thinning (de Kroon and Kalliola 1995; de Kroon 2005). However, integrated clones are also known to regulate density by suppressing rhizome bud formation, and through senescence of ramets in resource-poor areas (Alpert and Mooney 1986; Piqueras et al. 1999; de Kroon 2005).

We did observe these forces at work in the bamboo in our study plots – especially when comparing the relatively young stand of PLLAU to the more mature stand of PLLGL. Compared to other species, PLLAU had greatly increased densities of live and total ramets (Table 3.1, 3.8, 3.12). Both recruitment and mortality were increased, reflected in greater proportions of live shoots (Table 3.12) and greater absolute densities and proportions of dead mature ramets and total dead ramets (Table 3.12), especially when compared to PLLRU. We propose that both aforementioned processes – competition and clonal regulation – are at work in the bamboo in our experimental plots. The first would explain much of early colony development, in particular the extremely high densities followed by drastic mortality of older ramets in PLLAU. Although death of disadvantaged ramets to recover resources for the rest of the clone is typical of physiologically integrated genets, this extreme degree of ramet recruitment and then mortality seems like a waste of resources and counterintuitive to genet-level fitness; instead, ramet-to-ramet competition appears to dominate. During the latter phases of colony development, clonal integration and regulation seem to be the dominant forces during the latter phases of colony development, when suppression of ramet natality may be observed through greatly reduced and stable shoot recruitment (e.g., PLLGL; Table 3.12).

One reason for these early density-dependent processes in PLLAU may be a high degree of competitive interaction between neighboring clones, rather than competition between individual ramets of the same clone (which makes no sense). Given the closely-planted nature of the MZ bamboo farm, it is likely that neighboring ramets may arise from different clones, resulting in a classic scenario of exploitative competition among individuals. In such a case, individual ramets could be competing not only for sunlight access, but also for soil resources such as water and nutrients, all of which could affect ramet survival and therefore density.

Furthermore, in bamboos, the degree of lateral expansion seems to play a role in which mechanism of density regulation takes precedence: those that expand out rapidly show more reliance on regulation of ramet natality to limit density; those that show little horizontal expansion (e.g., tillering spp.) are subject to self-thinning, because canopy occlusion can affect an entire genet. Again, because bamboo at the farm is planted close together, and particularly because it is contained in mowed strips, even though *Phyllostachys* is capable of a great degree of lateral expansion, rhizomes are constantly running into neighboring clones as they push outward from their own—in a sense, artificially creating a situation that resembles lack of expansion.

The historic maintenance of mowed strips in bamboo stands may also exacerbate the problem of competition by triggering overactive and misplaced clonal dynamics. In the standard case of clonal regulation, ramet production is negatively correlated with stand density. In the case of PLLAU, such high density should cause this regulation to come into play, limiting the size of the shoot crop; but because large open areas still existed in the mowed spaces, recruitment continued to be extreme on the edges of

bamboo stands. In our research enclosures, however, mowing ceased after initiation of the study, and canopy closure by spring 2008 was nearly complete. Predictions under such a scenario would include restoration of clonal regulation of ramet recruitment, and reduced shoot production. In Year 3, proportional recruitment of PLLAU was indeed reduced (Table 3.12).

A number of ways exist in which aboveground disturbance may impact subsequent recruitment and biomass production in clonal systems. The degree and manner in which subsequent changes manifest in vegetative structure depend largely on the degree and manner of the disturbance itself. In a broad sense, any interference with normal within-year nutrient cycling and source-sink dynamics may affect recruitment, survival, and production. As discussed previously, disturbance tends to cause depletion of stored belowground nutrients, particularly carbohydrates (Zasada et al. 1994; Tschaplinski and Blake 1995; Reichenbacker et al. 1996; Landhausser and Lieffers 1997, 2002; Li et al. 1998a,b). This could in turn impair normal annual patterns of bamboo-stand growth and development

Disturbance could take the form of defoliation, through vertebrate or invertebrate herbivory, or factors that could increase leaf senescence. Excess removal of leaves, especially in a canopy that is balanced with respect to the typical 2-year life cycle of most woody bamboo leaves, could reset an entire canopy to the same leaf age. This could catalyze unstable swings in leaf-to-ramet ratios and photosynthetic capacity, creating a glut of resources when all leaves are new and at peak photosynthesis, followed by severe resource restriction when all leaves shed at the same time 2 years later (Li et al. 1998 a,b; Kleinhenz and Midmore 2001).

Disturbance could also take the form of complete ramet removal. If ramet clipping is sporadic and widely distributed, the genet may be able to absorb the effects with little impact on future production – this is, indeed, the advantage of clonal systems. Giant panda herbivory could autumn into this category, as the animals do sever most of the ramet from its base, but practice their characteristically extreme diet selection, and thus pick and choose a few ramets from those available (Wang et al. 2007). Particularly if physiological integration among ramets is inactive, this sort of disturbance could have minimal effects on the rest of the clone (Wang et al. 2007).

If, however, total ramet removal is more widespread or greater in magnitude, more extreme effects on regrowth could occur. We have observed such phenomena at the AgriCenter bamboo farm, in plots other than those in which our study enclosures were located. Clear cutting of 0.05- to 0.15-ha sections of bamboo resulted, the following spring, in a phenomenon we colloquially call "asparagus growth": very dense production of extremely short, thin culms, with greatly increased numbers of branches per ramet and heavy leafing. The proximate physiological cause of this change in morphology could of course be attributed to classical hormone-mediated apical release (Gurevitch et al. 2002). As to the selective advantage of such a response, two possibilities exist. At first glance, the response of bamboo in such a case is similar to the classical compensatory-growth response of many herbaceous grasses, which often respond to clipping by shifting to a prostrate growth form with high rates of vegetative propagation (Wilsey 2002). Shoot production, rhizome growth, and nutrient storage are promoted, and net primary productivity increases (Wilsey 2002). However, this response is seen primarily in grasses that receive chronic, moderate aboveground disturbance

(Wilsey 2002), rather than a single catastrophic event. Furthermore, evidence for the so-called "overcompensation" of grasses to disturbances such as herbivory is equivocal (Belsky et al. 1993), and it is unclear how much this hypothesis applies to non-herbaceous bamboos, which seem to respond similarly to woody shrubs and trees with regard to disturbance (Tripathi and Singh 1994; Shanmughavel and Francis 1996). A more likely second explanation involves the importance of clonal dynamics and source-sink processes.

Immediately following the catastrophic removal of the aboveground source of photosynthate, along with any stored resources in aboveground vegetation, root:shoot ratios in the remaining clone are dramatically reversed, and the genet undergoes a crisis of resource availability. Belowground structures continue to respire and use stored resources, but are themselves non-productive; a source of photoassimilates must be rapidly reestablished to ensure continued survival of the clone. Because (1) belowground stores are not sufficient to support regrowth of prior growth forms (i.e., tall, large-diameter culms), (2) increased surface area for photosynthesis is essential, necessitating a drastic increase in leaf area, and (3) complete loss of the overstory canopy removes the need to grow so tall to achieve access to sunlight, regrowth is severely stunted but heavily leaved. During this initial regrowth phase, carbon fixation is rapid and large-scale, and photoassimilates are immediately and preferentially transported belowground (Kleinhenz and Midmore 2001) to replenish the colony's stores that were depleted during the production of "asparagus" growth. The maintenance of belowground structures at all costs is an important trait of long-lived clonal species, since survival of belowground biomass ensures survival of the genet; without the physiological integration, carbohydrate

and nutrient stores, and structural support provided by the rhizomes, the clone could not persist (Kleinhenz and Midmore 2001).

It is important to note that the timing of such a large aboveground disturbance will have a significant effect on the rate and form of regrowth to follow. If a bamboo stand is clear-cut or burned in late autumn or winter, when belowground carbohydrate stores are at their maximum, the clone will have a significant reserve from which to mobilize resources to support new shoots. However, if the disturbance occurs in late spring, when belowground reserves have been drained by the annual shoot crop, the remaining rhizome structure will represent a sink, with few reserves but a large respiratory demand (Tripathi and Singh 1994; Li et al. 1998a,b; Shanmughavel and Francis 1996, 2001; Kleinhenz and Midmore 2001). Aboveground growth following this event will be slow as long as the root:leaf ratio is so unbalanced, since photosynthates will be preferentially transported belowground to replenish stores and maintain tissues. Extensive rhizome mortality may even occur if belowground reserves are too depleted at the time of disturbance; this would reduce the area occupied by the remaining genet, but it would help to restore the proper root:leaf ratio and promote persistence of the remaining clone (Tripathi and Singh 1994; Li et al. 1998a,b; Shanmughavel and Francis 1996, 2001).

In Year 2 (2006 to 2007), two stochastic events occurred which may have produced interesting consequences for our ongoing study. In summer 2006, the study site received less rainfall than the previous year, especially during the period of peak temperatures (Table 3.3, Fig. 3.4). In spring 2007, seasonal severe weather and accompanying rainfall was less than in 2006 or 2008. During winter 2006 to 2007, Shelby County experienced a stochastic peak in the local population of red-winged

blackbirds (*Agelaius phoeniceus*). Because of this species' tendency to form large communal flocks in winter, and the attraction of the MZ bamboo stands as a sheltered roosting location among agricultural fields, thousands of birds descended upon our study site each night between November and February. The resulting deposition of guano was impressive, covering the soil surface between bamboo rows with 2 to 5 cm of organic matter by late January, and coating most ramets with notable concretions of urates.

For ramets emerging as shoots in 2007, contrary to expected growth patterns already described, we observed a decrease in almost all measures of biomass production and bamboo-stand growth (residual biomass, ramet height, bottom branch height, basal culm diameter, and total ramet dry mass; Tables 3.5, 3.6, 3.7; Figs. 3.5 through 3.9). We propose that these changes were subject to the same forces as the production of "asparagus growth" previously discussed. Events of 2006 to 2007 did not remove entire ramets, but they did result in significant defoliation (see leaf dry mass, Tables 3.8, 3.9, 3.10, Fig. 3.10), impairing production of photoassimilates and corresponding nutrient stores, and again underscoring the importance of total canopy leaf area on subsequent biomass production (Reichenbacker et al. 1996; Li et al. 1998 a,b; Kleinhenz and Midmore 2001). The doubling of shoot recruitment rates for PLLRU in that same year (Table 3.12) may be an attempt by the clone to recuperate total leaf area in the stand: the growth of many more culms of smaller diameter means that leaf area per unit of total biomass is maximized.

Because we were unable to conduct a full ANCOVA analysis, it is difficult to determine whether either event (drought or blackbirds) contributed more or less to 2007 growth patterns. However, because the influx of blackbirds occurred after belowground

stores would have been established in autumn 2006, we presume that the drought conditions had a greater effect on subsequent biomass production. The large deposition of bird guano did, however, appear to have wide-sweeping effects on soil chemistry and nutritional composition of vegetation in 2007 (this study, unpublished data), and may have indeed contributed to the recovery in residual biomass, ramet height, and culm diameter we observed in spring 2008 (Table 3.5, 3.6, 3.7; Figs. 3.5, 3.6, 3.7), together with the already-discussed increase in leaf-to-ramet ratios (Tables 3.5, 3.6, 3.7; Fig. 3.10).

We would have been interested to continue this study past this 3-year span of time, to observe subsequent effects of such large-scale defoliation on leaf cycling and ramet recruitment in following years. Li et al. (1998 a,b) and Kleinhenz and Midmore (2001) predict that leaf lifespan would have reset for a large portion of the canopy, catalyzing a biennial boom-bust oscillation as leaves grown in 2007 are shed en masse after their second year. Thus, the winter of 2008 to 2009 would have witnessed a similar large-scale defoliation, seemingly in the absence of external forces. Ostensibly, with recruitment of new ramets in the intervening and following years, canopy leaf ages would eventually even out, and growth dynamics of the stand would stabilize. In the meantime, however, the stand would experience a large drop in production in 2009, and potentially again in 2011 (Reichenbacker et al. 1996). This could have serious consequences for those depending on the stand for a continuous supply of animal forage. Additionally, if the same amount of harvest pressure were maintained in the "off" years, a compounding of disturbance effects could occur, exacerbating the original impacts on production and potentially threatening genet survival. Such total-clone collapses have already been

observed in other institutions managing bamboo for giant pandas and other exotics (Reed 2009).

Such responses in vegetation to large-scale habitat destruction could likewise pose dire consequences for conservation of free-ranging populations of giant pandas, which already live on a knife-edge in terms of overall nutrient availability. Because they rarely experience a surplus of digestible energy, pandas do not often generate fat stores like other bears (Edwards et al. 2006); thus, this species cannot tolerate an "off year". The most immediate result would be failure to reproduce in such years: either physiological down-regulation of steps leading to conception, failure to bring a fetus to term, or failure to produce sufficient milk for neonatal survival. Low reproductive rates are already a significant roadblock to recovery of this species (Schaller et al. 1985). At the extreme, such an "off year" could result in nutritional deficiencies in adult pandas, or even starvation. Schaller et al. (1985) documented large-scale changes to bamboo life-cycle events as a result of logging in giant panda habitat, indicating a clear possibility for long-term compromise of forage availability with such activities.

We observed few differences among disturbance treatments in any measures of biomass production, recruitment, or mortality (Tables 3.4, 3.12), though we did see 2 interesting outcomes. The disturbance effects we observed on dry branch and culm mass in PLLRU may indicate that, at least for this species, a moderate amount of disturbance is desirable. Intermediate disturbance is known in many plant species to promote growth and recruitment, due to beneficial effects of canopy release and sunlight availability (Gurevitch et al. 2002). In this same fashion, PLLRU ramets in the 3%-annual-removal treatment seemed to respond positively, in terms of biomass production per ramet.

However, branches and culms in the 20%-annual-removal treatment returned to dry masses similar to control samples, suggesting that previously-discussed negative effects on biomass production may have cancelled out any potential benefits.

In the end, however, the effects of our planned disturbance treatments seemed minimal, compared to the effects of larger-scale events beyond our control. It is possible that the disturbance intensities applied in this study were still below the threshold of sustainability. Furthermore, as already discussed, timing of disturbance matters a great deal in clonal species. Because we were interested in creating a model for sustainable harvest, we administered biomass removal in a uniform, diffuse fashion. The same amount of disturbance, administered in a non-uniform manner – ie., removal of the same number of ramets in a concentrated area – might have resulted in very different responses in regrowth and surrounding vegetation.

Many clonal species are able to mitigate the effects of disturbance or mount a defensive response by taking advantage of physiological integration and sharing of resources among ramets (Herms and Mattson 1992; Gough et al. 2002; Peltzer 2002; Wilsey 2002; Stuefer 2004). However, evidence for clonal integration in bamboos varies. Ramets of dwarf bamboo (*Sasa* spp.) do appear to communicate, enabling support of ramets in resource-poor patches by those in resource-rich areas (Saitoh et al. 2002). Wang et al. (2007), on the other hand, failed to detect any evidence of clonal dynamics in structural response to herbivory. They suggested that culms were acting as individuals, with hormonally mediated compartmentalization of stressed portions of the clone (Haukioja 1991). The ability of clonal plants to regulate and vary the degree of

physiological integration among ramets complicates attempts to characterize disturbance effects.

Although the subplots from which we harvested bamboo were randomized in location, they were in potentially close physical proximity to each other and to control subplots. Dye techniques have been used to identify closely-spaced sister ramets, however a method does not yet exist to identify members of an entire clone [W. Wang and S. B. Franklin, University of Memphis, personal communication] – particularly in rhizomatous rather than tillering bamboo species, where sister ramets can be physically distant. Thus, it is very possible that portions of clones in our study straddled subplots. If no physiological integration occurred in these clones, as in Wang et al. (2007), then our subplots were truly independent. However, if this were the case, we would also expect remaining ramets to behave as if no disturbance occurred. If, on the other hand, integration were occurring, disturbance effects may have been mitigated or spread over a larger area, confounding our results. The only true way to parse these two possibilities would be to plant a bamboo stand such that clones do not overlap, or to identify members of a clone and space treatments out sufficiently that two treatments did not affect a single clone. As we were working in a relatively small (0.4-ha), already-established stand, neither experimental design was possible.

Of the primary bamboo consumers listed in our introduction to this paper, all face some degree of habitat loss or modification. The key to conservation is habitat restoration (WWF 2004): expanding existing refuges, and establishing protected corridors to allow gene flow among isolated populations (Hunter et al. 2003). However, to do so without consideration for the nutritional environment is to set these animals up for

failure. Factors such as year-to-year clonal growth dynamics, seasonal nutrient flux, and potential effects of disturbance – especially with regard to scale and timing of biomass removal – have direct impact on the availability and nutritional quality of forage in a natural bamboo forest. By using the giant panda's relationship to its food source as a model, we hope to expand our understanding of bamboo management for a number of endangered or threatened species in captive-housed institutions. Similar studies on disturbed bamboo in the wild would be essential to management and conservation of free-ranging animal species that depend on bamboo habitats for survival. Schaller et al. (1985) did report altered bamboo recruitment and production cycles in response to logging in giant panda habitat. A closer scrutiny of these processes is merited, throughout the giant panda's native range.

Table 3.1 Initial parameters of bamboo stands

Species	Enclosure[2]	Max canopy height (m)	Mean (standard error)[1] Sampled ramet height (cm)	Basal culm diameter[3] (mm)	Total ramet density (# per m^2)	Live mature ramet density (# per m^2)
PLLAU[4]	A	4.95	411.33 (9.41)	14.00 (2.08)	48.67 (19.19)	34.67 (10.37)
	B	4.11	375.07 (21.01)	13.57 (1.24)	34.67 (9.77)	31.33 (8.21)
	C	4.22	389.47 (18.94)	14.07 (0.35)	41.33 (7.36)	31.67 (6.23)
	D	5.00	371.27 (18.49)	13.73 (0.66)	38.33 (3.53)	27.67 (4.37)
PLLGL[5]	A	6.40	490.30 (22.31)	23.60 (4.16)	11.00 (1.15)	7.00 (1.53)
	B	6.40	491.80 (19.57)	26.00 (0.58)	9.67 (2.40)	8.33 (2.03)
	C	6.10	526.13 (69.70)	21.33 (3.67)	17.00 (6.51)	15.00 (5.03)
	D	6.10	533.10 (31.10)	18.00 (1.63)	8.33 (2.96)	7.67 (2.73)
PLLRU[6]	A	5.95	491.67 (23.70)	17.07 (1.51)	11.67 (3.38)	11.33 (3.71)
	B	7.01	477.33 (32.31)	17.50 (0.93)	27.33 (5.61)	23.67 (6.17)
	C	5.95	455.33 (36.13)	13.90 (0.59)	18.00 (9.54)	16.00 (9.45)
	D	5.79	478.33 (25.23)	12.37 (1.50)	21.50 (0.41)	20.00 (1.63)

[1]Recorded at study initiation (1-Jul-05 for PLLAU; 17-Sept-05 for PLLGL and PLLRU), except where noted.
[2]Four replicate enclosures per species were fenced off for the length of the study, with duplicated experimental treatments applied to subplots therein.
[3]Measured for all species on 13-Nov-05.
[4]*Phyllostachys aureosulcata.*
[5]*Phyllostachys glauca.*
[6]*Phyllostachys rubromarginata.*
Note: All data recorded at the Shelby County AgriCenter, Memphis, Tennessee, USA.

Table 3.2 Annual soil tests and fertility regime.

				Extractable nutrients (kg/ha)						Nutrient appication (kg/ha/yr)			
Species[1]	Date	pH	CEC[2]	P	K	Ca	Mg	Zn	Na	Lime	N	P205	K20
PLLAU	May 2005	6.2	6.7	62.5	119.3	1847	93.2	2.16	63.64	0	68	34	68
	Oct 2006	5.1	6.7	106.8	181.8	1323	126.1	4.77	78.41	5114	68	0	0
	Oct 2007	4.8	8.1	314.8	662.5	1433	150.0	7.50	103.41	6818	68	0	0
PLLGL	May 2005	6.2	6.7	60.2	108.0	1716	95.5	2.50	29.55	0	68	34	68
	Oct 2006	5.1	7.6	129.5	206.8	1476	158.0	5.80	93.18	6818	68	0	0
	Oct 2007	4.6	8.1	321.6	606.8	1366	200.0	7.16	120.45	6818	68	0	0
PLLRU	May 2005	5.8	6.4	77.3	137.5	1303	98.9	2.61	13.64	5114	68	34	34
	Oct 2006	4.7	7.0	205.7	280.7	1036	126.1	5.34	92.05	6818	68	0	0
	Oct 2007	4.5	9.3	590.9	685.2	1681	193.2	6.36	107.95	6818	68	0	0

[1]PLLAU = *Phyllostachys aureosulcata*; PLLGL = *P. glauca*; PLLRU = *P. rubromarginata*.
[2]Cation-exchange capacity, cmol H+/kg
Notes: Soil samples were taken in October of each year from 0.4-ha monoculture bamboo plots at the Shelby County AgriCenter, Memphis, Tennessee, USA. Two locations were sampled per replicate enclosure (8 locations per plot), and pooled by bamboo species for analysis at the Mississippi State University Cooperative Extension Service (MCES) Soil Testing Laboratory. Subsequent fertilizer application in November and January/February of each year was performed according to MCES recommendations for temperate forage grasses.

Table 3.3 Weather data for study period.

Year	Month	Total precipitation (cm)	Mean temperature (°C)
2005	May	0.78	19.9
	Jun	2.29	25.5
	Jul	5.99	27.2
	Aug	4.05	28.4
	Sep	1.37	24.7
	Oct	0.43	16.2
	Nov	2.08	11.9
	Dec	1.54	3.9
2006	Jan	5.08	8.3
	Feb	2.75	3.8
	Mar	2.36	11.4
	Apr	3.02	19.4
	May	2.85	21.3
	Jun	1.90	25.2
	Jul	0.37	27.9
	Aug	2.25	28.8
	Sep	2.00	21.9
	Oct	1.81	15.9
	Nov	1.91	10.4
	Dec	4.40	8.0
2007	Jan	3.13	5.3
	Feb	1.60	4.3
	Mar	0.41	16.3
	Apr	2.66	14.8
	May	0.69	22.9
	Jun	1.50	26.6
	Jul	2.87	26.8
	Aug	0.56	30.4
	Sep	1.28	24.60
	Oct	3.27	18.90
	Nov	2.65	11.30
	Dec	3.00	7.90
2008	Jan	3.15	3.90
	Feb	1.93	6.50
	Mar	5.66	10.80
	Apr	7.07	15.20
	May	5.05	20.90
	Jun	1.64	26.70
	Jul	0.98	27.70
	Aug	2.74	26.00

Note: All data were taken from a NOAA weather station located at Shelby County AgriCenter, Memphis, Tennessee, USA (35° 7'47"N, 89°48'13"W), 2.5 km from the study site.

Table 3.4 Aboveground disturbance effects on *P. rubromarginata* biomass production.

	Branch dry mass (kg)		Culm[3] dry mass (kg)	
Disturbance treatment[1]	Mean[2]	N	Mean	N
Control	0.094[a]	136	0.343[ab]	136
3%	0.108[b]	137	0.378[b]	137
20%	0.098[ab]	135	0.335[a]	135
SEM[4]	0.018		0.048	
F[5] (num df, denom df)	3.71 (2,308)		3.02 (2,350)	
P[6]	0.03		0.05	

[1]Aboveground disturbance treatments (administered quarterly) are as follows: control (no bamboo removal), 3% annual removal of live individual ramets, and 20% annual removal.
[2]Lettered superscripts indicate differences within columns ($P < 0.05$).
[3]Culm = central, woody stem of bamboo.
[4]Maximum standard error of the mean.
[5]F ratio (numerator degrees of freedom, denominator degrees of freedom) for split-plot repeated-measures Analysis of Variance of disturbance treatment.
[6]P-value for split-plot repeated-measures Analysis of Variance of disturbance treatment.
Notes: Data were recorded at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2008. Means are shown for significant Analyses of Variance (PROC MIXED; SAS Institute 2012) in a split-plot repeated-measures design, with replicate enclosure as the repeated unit, sampling date as the main-plot factor (adjusted for effects of ramet age), and disturbance treatment as the subplot factor.

Table 3.5 Biomass production and stand maturity by ramet cohort and sampling date: *Phyllostachys aureosulcata.*

	Residual biomass[1]								
	2005[2]		2006		2007		2008		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
1-Jul-05									
6-Sep-05									
12-Nov-05	0.004	12							0.0113
10-Jan-06	-0.011	12							0.0084
19-Mar-06	0.020	12							0.0122
28-Apr-06, 15 to 45-cm shoots			-0.098	12					0.0007
28-Apr-06, 1-m shoots			-0.094	12					0.0007
26-May-06	0.014[a]	12	-0.060[b]	12					0.0115
1-Jul-06	0.009	12	-0.009	12					0.0141
6-Sep-06	0.019	12	0.027	12					0.0149
12-Nov-06	0.030	12	0.023	12					0.0169
30-Jan-07	-0.003	11	0.017	10					0.0122
18-Mar-07	0.080[a]	10	0.048[b]	12					0.0110
4-Apr-07, 15 to 45-cm shoots					-0.097	12			0.0003
4-Apr-07, 1-m shoots					-0.098	12			0.0004
11-May-07	0.042[a]	11	0.041[a]	11	-0.080[b]	12			0.0145
21-Jun-07	0.024[a]	11	0.030[a]	12	-0.031[b]	12			0.0127
24-Aug-07	0.026[a]	11	0.057[b]	12	-0.003[c]	12			0.0136
3-Dec-07	0.039[a]	12	0.047[a]	12	-0.037[b]	12			0.0151
14-Feb-08	0.012[a]	6	0.035[a]	6	-0.039[b]	6			0.0182
11-Apr-08	0.053[a]	6	0.053[a]	6	-0.021[b]	6			0.0267
9-May-08, 15 to 45-cm shoots							-0.095	6	0.0006
9-May-08, 1-m shoots							-0.097	6	0.0008
30-May-08	0.042[a]	6	0.051[a]	6	-0.040[b]	6	-0.073[b]	6	0.0190

ANOVA statistics, including all ramet cohorts

Interaction, sampling date x ramet age

F (num df, denom df)	6.53 (18,381)
P	< 0.001

Table 3.5 (Continued)

	Ramet height (cm)								
	2005[2]		2006		2007		2008		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
1-Jul-05	386.78	12							8.85
6-Sep-05	377.88	12							7.96
12-Nov-05	334.08	11							12.19
10-Jan-06	300.53	11							20.29
19-Mar-06	338.08	12							20.59
28-Apr-06, 15 to 45-cm shoots			22.89	12					0.57
28-Apr-06, 1-m shoots			103.50	12					1.95
26-May-06	343.57[a]	12	409.67[b]	12					19.57
1-Jul-06	331.42[a]	11	411.75[b]	12					21.56
6-Sep-06	357.17[a]	12	455.00[b]	12					20.47
12-Nov-06	379.83[a]	12	423.17[b]	12					22.03
30-Jan-07	342.92[a]	12	401.85[b]	9					20.76
18-Mar-07	406.42[a]	12	447.08[b]	12					17.87
4-Apr-07, 15 to 45-cm shoots					29.18	12			0.58
4-Apr-07, 1-m shoots					102.42	12			1.48
11-May-07	368.50[a]	12	416.43[b]	11	389.50[ab]	12			17.06
21-Jun-07	380.08[a]	12	448.67[b]	12	408.67[a]	12			12.44
24-Aug-07	398.66[ab]	11	434.67[a]	12	393.75[b]	12			14.92
3-Dec-07	429.00[a]	12	441.67[a]	12	382.92[b]	12			15.94
14-Feb-08	380.52	6	412.02	6	372.69	6			22.24
11-Apr-08	395.19	6	426.52	6	380.86	6			30.77
9-May-08, 15 to 45-cm shoots							37.28	6	0.87
9-May-08, 1-m shoots							106.19	6	1.94
30-May-08	430.86[ab]	6	464.86[a]	6	371.86[c]	6	413.36[bc]	6	28.23

ANOVA statistics, including all ramet cohorts

Interaction, sampling date x ramet age

F (num df, denom df)	5.82 (18,404)
P	< 0.001

Table 3.5 (Continued)

	Basal culm[5] diameter (mm)								
	2005[2]		2006		2007		2008		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
1-Jul-05									
6-Sep-05									
12-Nov-05	13.84	12							0.544
10-Jan-06	12.19	12							0.584
19-Mar-06	13.58	12							0.566
28-Apr-06, 15 to 45-cm shoots			15.07	12					0.393
28-Apr-06, 1-m shoots			17.03	12					0.530
26-May-06	13.19[a]	12	17.01[b]	12					0.744
1-Jul-06	12.59[a]	12	15.86[b]	12					0.764
6-Sep-06	12.83[a]	12	18.44[b]	12					0.960
12-Nov-06	13.63[a]	12	17.09[b]	12					0.588
30-Jan-07	12.42[a]	12	15.00[b]	10					0.836
18-Mar-07	14.45[a]	11	18.00[b]	12					0.936
4-Apr-07, 15 to 45-cm shoots					13.53	12			0.352
4-Apr-07, 1-m shoots					14.26	12			0.514
11-May-07	13.20[a]	11	15.99[b]	11	13.54[a]	12			0.924
21-Jun-07	13.57[a]	12	17.36[b]	12	13.83[a]	12			0.725
24-Aug-07	14.41[a]	11	16.86[b]	12	14.81[a]	12			0.867
3-Dec-07	15.18[a]	12	18.33[b]	12	13.16[c]	12			1.060
14-Feb-08	12.48[a]	6	15.51[b]	6	12.15[a]	6			0.630
11-Apr-08	14.53	6	16.08	6	14.22	6			0.975
9-May-08, 15 to 45-cm shoots							14.36	6	0.481
9-May-08, 1-m shoots							15.00	6	0.475
30-May-08	15.13[ab]	6	18.12[a]	6	13.24[b]	6	14.27[b]	6	0.978

ANOVA statistics, including all ramet cohorts

Interaction, sampling date x ramet age

F (num df, denom df)	11.90 (18,384)
P	< 0.001

Table 3.5 (Continued)

	Height of lowest branch (cm)								
	2005[2]		2006		2007		2008		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
1-Jul-05									
6-Sep-05									
12-Nov-05	73.12	12							8.28
10-Jan-06	87.08	12							6.69
19-Mar-06	84.67	12							8.82
28-Apr-06, 15 to 45-cm shoots									
28-Apr-06, 1-m shoots									
26-May-06	80.83[a]	12	131.92[b]	12					10.40
1-Jul-06	100.37[a]	11	161.08[b]	12					13.30
6-Sep-06	103.08[a]	12	179.21[b]	11					17.80
12-Nov-06	124.58[a]	12	181.25[b]	12					10.92
30-Jan-07	83.82[a]	11	148.53[b]	9					12.62
18-Mar-07	128.19[a]	11	171.42[b]	12					11.00
4-Apr-07, 15 to 45-cm shoots									
4-Apr-07, 1-m shoots									
11-May-07	97.97[a]	11	153.37[b]	11	127.25[ab]	12			11.50
21-Jun-07	120.08[a]	12	203.67[b]	12	151.10[c]	11			13.58
24-Aug-07	111.82[a]	11	164.67[b]	12	139.75[ab]	12			14.97
3-Dec-07	140.67[a]	12	179.33[b]	12	141.17[a]	12			14.89
14-Feb-08	117.38	6	152.38	6	114.38	6			13.38
11-Apr-08	131.72	6	159.55	6	129.05	6			22.07
9-May-08, 15 to 45-cm shoots									
9-May-08, 1-m shoots									
30-May-08	129.88	6	182.88	6	114.05	6	184.55	6	21.74

ANOVA statistics, including all ramet cohorts

Interaction, sampling date x ramet age

F (num df, denom df)	7.66 (18,325)
P	< 0.001

Table 3.5 (Continued)

	Ramet dry mass (kg)								
	2005[2]		2006		2007		2008		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
1-Jul-05	0.224	12							0.018
6-Sep-05	0.270	12							0.016
12-Nov-05	0.226	12							0.026
10-Jan-06	0.178	12							0.017
19-Mar-06	0.257	12							0.029
28-Apr-06, 15 to 45-cm shoots			0.028	12					0.002
28-Apr-06, 1-m shoots			0.043	12					0.002
26-May-06	0.247[a]	12	0.131[b]	12					0.033
1-Jul-06	0.226	12	0.240	12					0.032
6-Sep-06	0.241[a]	12	0.440[b]	12					0.069
12-Nov-06	0.278	12	0.346	12					0.041
30-Jan-07	0.195	11	0.285	10					0.039
18-Mar-07	0.375	11	0.453	12					0.038
4-Apr-07, 15 to 45-cm shoots					0.027	12			0.001
4-Apr-07, 1-m shoots					0.027	12			0.001
11-May-07	0.300[a]	12	0.353[a]	12	0.062[b]	12			0.041
21-Jun-07	0.275[a]	11	0.390[b]	12	0.157[c]	12			0.056
24-Aug-07	0.275[a]	12	0.457[b]	12	0.238[a]	12			0.072
3-Dec-07	0.329[a]	12	0.517[b]	12	0.142[c]	12			0.081
14-Feb-08	0.225[ab]	6	0.327[a]	6	0.135[b]	6			0.046
11-Apr-08	0.345[a]	6	0.387[a]	6	0.196[b]	6			0.072
9-May-08, 15 to 45-cm shoots							0.040	6	0.002
9-May-08, 1-m shoots							0.039	6	0.002
30-May-08	0.340[a]	6	0.462[a]	6	0.148[b]	6	0.087[b]	6	0.073

ANOVA statistics, including all ramet cohorts

Interaction, sampling date x ramet age

F (num df, denom df)	10.65 (18,407)
P	< 0.001

Table 3.5 (Continued)

	Leaf dry mass (kg)						
	2005[2]		2006		2007		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
1-Jul-05	0.059	12					0.006
6-Sep-05	0.069	12					0.006
12-Nov-05	0.050	12					0.006
10-Jan-06	0.037	12					0.005
19-Mar-06	0.049	12					0.008
28-Apr-06, 15 to 45-cm shoots							
28-Apr-06, 1-m shoots							
26-May-06	0.069	12					0.009
1-Jul-06	0.048	12	0.058	12			0.010
6-Sep-06	0.042[a]	12	0.085[b]	12			0.017
12-Nov-06	0.051	12	0.056	12			0.011
30-Jan-07	0.025	11	0.031	10			0.008
18-Mar-07	0.033	11	0.021	12			0.009
4-Apr-07, 15 to 45-cm shoots							
4-Apr-07, 1-m shoots							
11-May-07	0.032	12	0.041	12			0.009
21-Jun-07	0.041[a]	11	0.076[b]	12	0.034[a]	12	0.017
24-Aug-07	0.035[a]	12	0.109[b]	12	0.046[a]	12	0.019
3-Dec-07	0.028[a]	12	0.096[b]	12	0.013[a]	12	0.021
14-Feb-08	0.018	6	0.041	6	0.015	6	0.014
11-Apr-08	0.012	6	0.043	6	0.011	6	0.014
9-May-08, 15 to 45-cm shoots							
9-May-08, 1-m shoots							
30-May-08	0.031[ab]	6	0.060[a]	6	0.016[b]	6	0.014

ANOVA statistics, including all ramet cohorts

Interaction, sampling date x ramet age

F (num df, denom df)	5.68 (15,326)
P	< 0.001

Table 3.5 (Continued)

	Branch dry mass (kg)						
	2005[2]		2006		2007		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
1-Jul-05	0.051	12					0.005
6-Sep-05	0.066	12					0.005
12-Nov-05	0.056	12					0.007
10-Jan-06	0.039	12					0.004
19-Mar-06	0.061	12					0.007
28-Apr-06, 15 to 45-cm shoots							
28-Apr-06, 1-m shoots							
26-May-06	0.055	12					0.008
1-Jul-06	0.052	12	0.042	12			0.008
6-Sep-06	0.056	12	0.067	12			0.013
12-Nov-06	0.060	12	0.046	12			0.009
30-Jan-07	0.046	11	0.047	10			0.007
18-Mar-07	0.073	11	0.064	12			0.010
4-Apr-07, 15 to 45-cm shoots							
4-Apr-07, 1-m shoots							
11-May-07	0.058	12	0.050	12			0.009
21-Jun-07	0.064[a]	12	0.055[a]	12	0.034[b]	12	0.008
24-Aug-07	0.064	12	0.072	12	0.057	12	0.011
3-Dec-07	0.074[a]	12	0.085[a]	12	0.031[b]	12	0.012
14-Feb-08	0.049	6	0.056	6	0.031	6	0.008
11-Apr-08	0.094[a]	6	0.078[ab]	6	0.057[b]	6	0.019
9-May-08, 15 to 45-cm shoots							
9-May-08, 1-m shoots							
30-May-08	0.073[a]	6	0.067[a]	6	0.034[b]	6	0.013

ANOVA statistics, including all ramet cohorts

Interaction, sampling date x ramet age

F (num df, denom df)	1.98 (15,327)
P	< 0.001

Table 3.5 (Continued)

	Culm[5] dry mass (kg)						
	2005[2]		2006		2007		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
1-Jul-05	0.114	12					0.007
6-Sep-05	0.135	12					0.008
12-Nov-05	0.120	12					0.016
10-Jan-06	0.101	12					0.009
19-Mar-06	0.147	12					0.016
28-Apr-06, 15 to 45-cm shoots							
28-Apr-06, 1-m shoots							
26-May-06	0.124	12					0.018
1-Jul-06	0.126	12	0.140	12			0.016
6-Sep-06	0.144[a]	12	0.288[b]	12			0.041
12-Nov-06	0.168[a]	12	0.244[b]	12			0.025
30-Jan-07	0.125[a]	11	0.206[b]	10			0.031
18-Mar-07	0.264[a]	12	0.368[b]	12			0.032
4-Apr-07, 15 to 45-cm shoots							
4-Apr-07, 1-m shoots							
11-May-07	0.209	12	0.263	12			0.025
21-Jun-07	0.169[a]	11	0.259[b]	12	0.090[c]	12	0.034
24-Aug-07	0.176[a]	12	0.276[b]	12	0.135[a]	12	0.043
3-Dec-07	0.227[a]	12	0.337[b]	12	0.098[c]	12	0.049
14-Feb-08	0.159[ab]	6	0.233[a]	6	0.090[b]	6	0.025
11-Apr-08	0.242[a]	6	0.268[a]	6	0.130[b]	6	0.040
9-May-08, 15 to 45-cm shoots							
9-May-08, 1-m shoots							
30-May-08	0.238[a]	6	0.336[a]	6	0.100[b]	6	0.050

ANOVA statistics, including all ramet cohorts

Interaction, sampling date x ramet age

F (num df, denom df)	12.62 (15,327)
P	< 0.001

[1]Residuals of the regression of measured ramet dry-matter biomass (kg) versus stem volume (ramet height x basal ramet diameter).

[2]Ramet cohort (year in which ramets emerged as shoots).

[3]Maximum standard error of the mean for compared least-square means

[4]Lettered superscripts indicate differences across rows ($P < 0.05$).

[5]Culm = central, woody stalk of bamboo

Notes: Data were collected at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2008. Least-square means are adjusted for other terms in the repeated-measures ANOVA model (PROC MIXED; SAS Institute 2012), with subplot as the repeated unit, testing for main effects and interaction of sampling date and ramet cohort.

Table 3.6 Biomass production and stand maturity by ramet cohort and sampling date: *Phyllostachys glauca.*

	Residual biomass[1]								
	2005[2]		2006		2007		2008		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
6-Sep-05									
12-Nov-05	-0.042	11							0.0182
10-Jan-06	0.047	12							0.0082
19-Mar-06	0.035	11							0.0105
28-Apr-06, 15 to 45-cm shoots			-0.100	12					0.0005
28-Apr-06, 1-m shoots			-0.104	12					0.0012
26-May-06	0.062[a]	12	-0.048[b]	12					0.0204
1-Jul-06	0.061[a]	12	-0.098[b]	12					0.0453
6-Sep-06	0.059[a]	12	-0.019[b]	12					0.0246
12-Nov-06	0.075[a]	12	-0.026[b]	12					0.0180
30-Jan-07	0.021[a]	9	-0.079[b]	9					0.0234
18-Mar-07	0.033[a]	12	-0.038[b]	12					0.0232
4-Apr-07, 15 to 45-cm shoots					-0.101	12			0.0015
4-Apr-07, 1-m shoots					-0.098	12			0.0014
11-May-07	0.032[a]	12	-0.040[b]	11	-0.031[b]	12			0.0200
21-Jun-07	0.019[a]	12	-0.067[b]	12	0.016[a]	12			0.0414
24-Aug-07	0.049	9	-0.003	9	0.038	7			0.0255
3-Dec-07	0.034[a]	12	-0.052[b]	12	-0.005[ab]	12			0.0355
14-Feb-08	0.058[a]	9	-0.034[b]	9	0.009[ab]	8			0.0331
11-Apr-08	0.039[a]	12	-0.028[b]	12	0.030[a]	12			0.0294
9-May-08, 15 to 45-cm shoots							-0.101	12	0.0011
9-May-08, 1-m shoots							-0.106	12	0.0014
30-May-08	-0.009[ab]	12	-0.084[c]	12	0.022[a]	12	-0.047[bc]	12	0.0430

ANOVA statistics, including all ramet cohorts

Interaction, sampling date x ramet age

F (num df, denom df)	6.88 (18,432)
P	< 0.001

Table 3.6 (Continued)

	Ramet height (cm)								
	2005[2]		2006		2007		2008		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
6-Sep-05	510.33	12							18.42
12-Nov-05	456.35	12							21.80
10-Jan-06	449.92	12							17.71
19-Mar-06	406.67	12							25.29
28-Apr-06, 15 to 45-cm shoots			25.73	12					1.09
28-Apr-06, 1-m shoots			103.17	12					3.19
26-May-06	556.58	12	614.00	12					19.00
1-Jul-06	482.92[a]	12	607.92[b]	12					36.11
6-Sep-06	523.92[a]	12	620.94[b]	11					26.12
12-Nov-06	485.92[a]	12	574.42[b]	12					38.52
30-Jan-07	503.38[a]	8	608.63[b]	9					35.29
18-Mar-07	493.75[a]	12	575.42[b]	12					31.11
4-Apr-07, 15 to 45-cm shoots					53.13	12			12.79
4-Apr-07, 1-m shoots					115.78	12			13.83
11-May-07	475.92[a]	12	611.67[b]	12	548.50[b]	12			22.70
21-Jun-07	493.00[a]	12	609.08[b]	12	490.25[a]	12			35.98
24-Aug-07	526.75[a]	12	620.92[b]	12	475.58[a]	12			33.63
3-Dec-07	555.42[a]	12	618.50[a]	12	435.67[b]	12			28.80
14-Feb-08	519.08[a]	9	607.85[b]	9	505.58[a]	8			38.46
11-Apr-08	526.50[a]	12	586.25[a]	12	448.50[b]	12			41.00
9-May-08, 15 to 45-cm shoots							31.39	12	0.35
9-May-08, 1-m shoots							98.17	12	3.12
30-May-08	519.25[a]	12	648.75[b]	12	495.25[c]	12	559.83[a]	12	34.74

ANOVA statistics, including all ramet cohorts

Interaction, sampling date x ramet age

F (num df, denom df)	9.36 (18,455)
P	< 0.001

Table 3.6 (Continued)

	Basal culm[5] diameter (mm)								
	2005[2]		2006		2007		2008		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
6-Sep-05									
12-Nov-05	22.33	11							1.59
10-Jan-06	16.88	12							0.80
19-Mar-06	16.43	12							0.97
28-Apr-06, 15 to 45-cm shoots			19.14	12					0.47
28-Apr-06, 1-m shoots			25.06	12					0.71
26-May-06	21.83	12	23.51	12					1.13
1-Jul-06	18.91[a]	12	25.00[b]	12					1.80
6-Sep-06	21.25	12	23.97	12					1.24
12-Nov-06	18.55[a]	12	21.91[b]	12					1.68
30-Jan-07	20.28[a]	9	26.72[b]	9					1.33
18-Mar-07	19.89[a]	12	23.57[b]	12					1.49
4-Apr-07, 15 to 45-cm shoots					13.51	12			0.42
4-Apr-07, 1-m shoots					13.67	12			0.65
11-May-07	20.54[a]	12	24.71[b]	11	19.70[a]	12			1.26
21-Jun-07	19.68[a]	12	23.91[b]	12	15.99[c]	12			1.74
24-Aug-07	20.77[a]	12	25.61[b]	12	17.06[c]	12			1.45
3-Dec-07	21.27[a]	12	23.65[a]	12	15.57[b]	12			1.74
14-Feb-08	19.47[a]	9	23.99[b]	9	16.56[a]	8			1.71
11-Apr-08	21.04[a]	12	23.14[a]	12	15.35[b]	12			1.66
9-May-08, 15 to 45-cm shoots							20.33	12	0.48
9-May-08, 1-m shoots							24.79	12	0.86
30-May-08	21.71[a]	12	25.10[b]	12	18.64[c]	12	22.15[a]	12	1.77

ANOVA statistics, including all ramet cohorts

Interaction, sampling date x ramet age

F (num df, denom df)	12.13 (18,444)
P	< 0.001

Table 3.6 (Continued)

	Height of lowest branch (cm)								
	2005[2]		2006		2007		2008		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
6-Sep-05	111.53	12							12.95
12-Nov-05	116.52	12							15.32
10-Jan-06	99.00	12							18.42
19-Mar-06	111.17	12							16.45
28-Apr-06, 15 to 45-cm shoots									
28-Apr-06, 1-m shoots									
26-May-06	174.08[a]	12	256.92[b]	12					17.28
1-Jul-06	134.58[a]	12	269.83[b]	12					14.89
6-Sep-06	186.67[a]	12	291.83[b]	12					16.85
12-Nov-06	159.00[a]	12	266.92[b]	12					20.92
30-Jan-07	144.15[a]	7	267.04[b]	9					28.01
18-Mar-07	174.83[a]	12	305.67[b]	12					17.73
4-Apr-07, 15 to 45-cm shoots									
4-Apr-07, 1-m shoots									
11-May-07	143.75[a]	12	317.57[b]	11	73.75[c]	12			18.88
21-Jun-07	187.58[a]	12	276.08[b]	12	133.00[c]	12			30.99
24-Aug-07	166.67[a]	12	275.75[b]	12	136.08[a]	12			21.10
3-Dec-07	204.17[a]	12	303.42[b]	12	119.33[c]	12			19.38
14-Feb-08	185.88[a]	9	353.69[b]	9	160.74[a]	8			25.60
11-Apr-08	191.92[a]	12	298.58[b]	12	131.08[c]	12			28.69
9-May-08, 15 to 45-cm shoots									
9-May-08, 1-m shoots									
30-May-08	195.75[a]	12	331.42[b]	12	117.25[c]	12	193.42[a]	12	29.12

ANOVA statistics, including all ramet cohorts

Interaction, sampling date x ramet age

F (num df, denom df)	24.54 (18,388)
P	< 0.001

Table 3.6 (Continued)

	Ramet dry mass (kg)								
	2005[2]		2006		2007		2008		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
6-Sep-05	0.558	12							0.073
12-Nov-05	0.418	12							0.070
10-Jan-06	0.413	12							0.044
19-Mar-06	0.385	11							0.047
28-Apr-06, 15 to 45-cm shoots			0.035	12					0.002
28-Apr-06, 1-m shoots			0.056	12					0.003
26-May-06	0.891[a]	12	0.381[b]	12					0.103
1-Jul-06	0.626	12	0.688	12					0.119
6-Sep-06	0.748	12	0.783	12					0.103
12-Nov-06	0.543	12	0.626	12					0.105
30-Jan-07	0.558	11	0.788	9					0.100
18-Mar-07	0.628	2	0.668	12					0.096
4-Apr-07, 15 to 45-cm shoots					0.009	15			0.003
4-Apr-07, 1-m shoots					0.028	14			0.003
11-May-07	0.564[a]	12	0.704[a]	12	0.291[b]	12			0.080
21-Jun-07	0.613[a]	12	0.839[b]	12	0.376[c]	12			0.153
24-Aug-07	0.650	9	0.803	9	0.640	7			0.117
3-Dec-07	0.788[a]	12	0.820[a]	12	0.300[b]	12			0.139
14-Feb-08	0.511[a]	9	0.837[b]	9	0.316[a]	8			0.145
11-Apr-08	0.789[a]	12	0.829[a]	12	0.321[b]	12			0.129
9-May-08, 15 to 45-cm shoots							0.065	17	0.004
9-May-08, 1-m shoots							0.072	17	0.006
30-May-08	0.709[a]	12	1.004[a]	12	0.414[b]	12	0.325[b]	12	0.155

ANOVA statistics, including all ramet cohorts

Interaction, sampling date x ramet age

F (num df, denom df)	6.06 (18,462)
P	< 0.001

Table 3.6 (Continued)

	Leaf dry mass (kg)						
	2005[2]		2006		2007		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
6-Sep-05	0.124	12					0.019
12-Nov-05	0.093	12					0.020
10-Jan-06	0.088	12					0.010
19-Mar-06	0.058	12					0.008
28-Apr-06, 15 to 45-cm shoots							
28-Apr-06, 1-m shoots							
26-May-06	0.205	12					0.028
1-Jul-06	0.141	12	0.098	12			0.022
6-Sep-06	0.155	12	0.113	12			0.041
12-Nov-06	0.082	12	0.069	12			0.016
30-Jan-07	0.039	11	0.027	9			0.011
18-Mar-07	0.030	12	0.002	12			0.009
4-Apr-07, 15 to 45-cm shoots							
4-Apr-07, 1-m shoots							
11-May-07	0.070	12	0.065	12			0.012
21-Jun-07	0.091	12	0.085	12	0.068	12	0.026
24-Aug-07	0.082	11	0.096	12	0.123	7	0.022
3-Dec-07	0.086	12	0.069	12	0.045	12	0.022
14-Feb-08	0.043	9	0.047	9	0.027	8	0.018
11-Apr-08	0.072	12	0.046	12	0.028	12	0.017
9-May-08, 15 to 45-cm shoots							
9-May-08, 1-m shoots							
30-May-08	0.068	12	0.106	12	0.076	12	0.031

ANOVA statistics, including all ramet cohorts

Main effect of ramet age

F^4 (num df, denom df)	2.57 (3,354)
P^5	0.054

Main effect of sampling date

F (num df, denom df)	9.39 (16,354)
P	< 0.001

Table 3.6 (Continued)

	Branch dry mass (kg)						
	2005[2]		2006		2007		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
6-Sep-05	0.110	12					0.015
12-Nov-05	0.069	12					0.013
10-Jan-06	0.081	12					0.009
19-Mar-06	0.077	12					0.007
28-Apr-06, 15 to 45-cm shoots							
28-Apr-06, 1-m shoots							
26-May-06	0.148	12					0.016
1-Jul-06	0.113	12	0.093	12			0.017
6-Sep-06	0.119	12	0.121	12			0.026
12-Nov-06	0.095	12	0.088	12			0.014
30-Jan-07	0.111	11	0.116	9			0.018
18-Mar-07	0.097	12	0.072	12			0.016
4-Apr-07, 15 to 45-cm shoots							
4-Apr-07, 1-m shoots							
11-May-07	0.092	12	0.090	12			0.010
21-Jun-07	0.095	12	0.119	12	0.090	12	0.031
24-Aug-07	0.110	12	0.123	12	0.097	11	0.031
3-Dec-07	0.130[a]	12	0.113[ab]	12	0.076[b]	12	0.033
14-Feb-08	0.083	9	0.093	9	0.056	8	0.022
11-Apr-08	0.134[a]	12	0.114[ab]	12	0.072[b]	12	0.022
9-May-08, 15 to 45-cm shoots							
9-May-08, 1-m shoots							
30-May-08	0.106	12	0.118	12	0.084	12	0.025

ANOVA statistics, including all ramet cohorts

Main effect of ramet age

F^4 (num df, denom df)	3.58 (3,359)
P^5	0.01

Main effect of sampling date

F (num df, denom df)	1.54 (16,359)
P	0.08

Table 3.6 (Continued)

	Culm[5] dry mass (kg)						
	2005[2]		2006		2007		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
6-Sep-05	0.324	12					0.043
12-Nov-05	0.256	12					0.041
10-Jan-06	0.244	12					0.029
19-Mar-06	0.253	11					0.038
28-Apr-06, 15 to 45-cm shoots							
28-Apr-06, 1-m shoots							
26-May-06	0.539	12					0.062
1-Jul-06	0.372	12	0.497	12			0.085
6-Sep-06	0.474	12	0.550	12			0.062
12-Nov-06	0.366	12	0.469	12			0.080
30-Jan-07	0.409[a]	11	0.648[b]	9			0.083
18-Mar-07	0.502	12	0.594	12			0.082
4-Apr-07, 15 to 45-cm shoots							
4-Apr-07, 1-m shoots							
11-May-07	0.403	12	0.549	12			0.061
21-Jun-07	0.427[a]	12	0.635[b]	12	0.218[c]	12	0.111
24-Aug-07	0.438[a]	10	0.596[a]	9	0.261[b]	12	0.074
3-Dec-07	0.572[a]	12	0.638[a]	12	0.180[b]	12	0.101
14-Feb-08	0.377[a]	9	0.700[b]	9	0.233[a]	8	0.110
11-Apr-08	0.583[a]	12	0.669[a]	12	0.221[b]	12	0.103
9-May-08, 15 to 45-cm shoots							
9-May-08, 1-m shoots							
30-May-08	0.536[a]	12	0.780[a]	12	0.255[b]	12	0.110

ANOVA statistics, including all ramet cohorts

Interaction, sampling date x ramet age

F (num df, denom df)	9.28 (15,354)
P	< 0.001

[1]Residuals of the regression of measured ramet dry-matter biomass (kg) versus stem volume (ramet height x basal ramet diameter).
[2]Ramet cohort (year in which ramets emerged as shoots).
[3]Maximum standard error of the mean for compared least-square means
[4]Lettered superscripts indicate differences across rows ($P < 0.05$).
[5]Culm = central, woody stalk of bamboo
Notes: Data were collected at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2008. Least-square means are adjusted for other terms in the repeated-measures ANOVA model (PROC MIXED; SAS Institute 2012), with subplot as the repeated unit, testing for main effects and interaction of sampling date and ramet cohort.

Table 3.7 Biomass production and stand maturity by ramet cohort and sampling date: *Phyllostachys rubromarginata.*

	Residual biomass[1]								
	2005[2]		2006		2007		2008		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
6-Sep-05									
12-Nov-05	0.009	12							0.0113
10-Jan-06	0.045	12							0.0127
19-Mar-06	0.039	12							0.0092
28-Apr-06, 15 to 45-cm shoots			-0.096	12					0.0008
28-Apr-06, 1-m shoots			-0.103	12					0.0010
26-May-06	0.113[a]	12	-0.037[b]	12					0.0093
1-Jul-06	0.070[a]	12	0.009[b]	12					0.0102
6-Sep-06	0.071	12	0.043	12					0.0213
12-Nov-06	0.072[a]	12	0.019[b]	12					0.0162
30-Jan-07	0.068[a]	11	0.033[b]	10					0.0107
18-Mar-07	0.059	11	0.033	12					0.0148
4-Apr-07, 15 to 45-cm shoots					-0.096	12			0.0006
4-Apr-07, 1-m shoots					-0.097	12			0.0006
11-May-07	0.060[a]	12	0.020[b]	12	-0.063[c]	12			0.0114
21-Jun-07	0.059[a]	12	0.037[a]	12	0.0002[b]	12			0.0156
24-Aug-07	0.067[a]	12	0.039[ab]	8	0.008[b]	12			0.0212
3-Dec-07	0.084[a]	12	0.042[b]	12	0.029[b]	12			0.0184
14-Feb-08	0.016[a]	8	0.063[b]	7	0.050[ab]	10			0.0169
11-Apr-08	0.064	12	0.037	12	0.037	12			0.0123
9-May-08, 15 to 45-cm shoots							-0.103	12	0.0008
9-May-08, 1-m shoots							-0.105	10	0.0009
30-May-08	0.078[a]	11	0.011[bc]	12	0.034[b]	11	-0.006[c]	9	0.0213

ANOVA statistics, including all ramet cohorts

Interaction, sampling date x ramet age

F (num df, denom df)	6.34 (18,436)
P	< 0.001

Table 3.7 (Continued)

	Ramet height (cm)								
	2005[2]		2006		2007		2008		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
6-Sep-05	475.67	12							13.29
12-Nov-05	398.62	12							12.54
10-Jan-06	479.42	12							17.43
19-Mar-06	452.08	12							23.36
28-Apr-06, 15 to 45-cm shoots			27.13	12					1.10
28-Apr-06, 1-m shoots			96.46	12					2.83
26-May-06	491.00	12	527.83	12					26.50
1-Jul-06	478.00[a]	12	537.68[b]	11					25.66
6-Sep-06	501.51[a]	11	574.75[b]	12					30.83
12-Nov-06	492.67	12	542.75	12					26.59
30-Jan-07	482.83[a]	12	561.86[b]	10					30.43
18-Mar-07	459.33[a]	12	533.67[b]	12					27.70
4-Apr-07, 15 to 45-cm shoots					35.05	12			0.74
4-Apr-07, 1-m shoots					111.46	12			2.47
11-May-07	480.25	12	509.33	12	459.51	11			24.34
21-Jun-07	450.58[a]	12	531.83[b]	12	454.17[a]	12			29.37
24-Aug-07	476.58[ab]	12	525.00[a]	12	465.50[b]	12			23.84
3-Dec-07	529.17[a]	12	551.75[a]	12	468.25[b]	12			24.17
14-Feb-08	474.80[a]	9	611.94[b]	7	502.80[a]	10			21.06
11-Apr-08	465.75	12	496.67	12	464.50	12			28.32
9-May-08, 15 to 45-cm shoots							32.30	12	0.52
9-May-08, 1-m shoots							96.28	10	7.36
30-May-08	518.05[a]	11	542.50[ab]	12	470.52[b]	11	590.42[c]	12	22.36

ANOVA statistics, including all ramet cohorts

Interaction, sampling date x ramet age

F (num df, denom df)	5.68 (18,454)
P	< 0.001

Table 3.7 (Continued)

	Basal culm[5] diameter (mm)								
	2005[2]		2006		2007		2008		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
6-Sep-05									
12-Nov-05	15.21	12							0.825
10-Jan-06	16.73	12							0.780
19-Mar-06	16.23	12							0.790
28-Apr-06, 15 to 45-cm shoots			17.51	12					0.345
28-Apr-06, 1-m shoots			23.69	12					0.559
26-May-06	17.23[a]	12	20.08[b]	12					0.667
1-Jul-06	16.03[a]	12	20.59[b]	12					0.566
6-Sep-06	17.13[a]	12	19.78[b]	12					1.192
12-Nov-06	18.27	12	19.18	12					0.959
30-Jan-07	17.71[a]	12	19.92[b]	10					0.909
18-Mar-07	16.18[a]	11	20.23[b]	12					0.911
4-Apr-07, 15 to 45-cm shoots					14.15	12			0.371
4-Apr-07, 1-m shoots					14.08	12			0.499
11-May-07	18.21[a]	12	19.52[a]	12	13.91[b]	12			0.914
21-Jun-07	16.26[a]	12	18.77[b]	12	14.23[c]	12			0.903
24-Aug-07	17.08[a]	12	20.97[b]	12	13.81[c]	12			0.746
3-Dec-07	18.89[a]	12	20.17[a]	12	14.80[b]	12			0.900
14-Feb-08	17.14[a]	9	20.87[b]	7	16.37[a]	10			1.443
11-Apr-08	16.76[a]	12	18.66[a]	12	14.74[b]	12			1.050
9-May-08, 15 to 45-cm shoots							20.75	12	0.464
9-May-08, 1-m shoots							24.27	10	0.928
30-May-08	18.76[a]	11	20.60[a]	12	13.57[b]	11	21.27[a]	12	1.011

ANOVA statistics, including all ramet cohorts

Interaction, sampling date x ramet age

F (num df, denom df)	16.76 (18,445)
P	< 0.001

Table 3.7 (Continued)

	Height of lowest branch (cm)								
	2005[2]		2006		2007		2008		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
6-Sep-05	122.55	12							13.81
12-Nov-05	76.30	12							11.74
10-Jan-06	122.97	12							12.06
19-Mar-06	111.50	12							15.36
28-Apr-06, 15 to 45-cm shoots									
28-Apr-06, 1-m shoots									
26-May-06	125.17[a]	12	214.67[b]	12					18.28
1-Jul-06	134.75[a]	12	246.50[b]	12					15.22
6-Sep-06	147.42[a]	12	249.83[b]	12					17.22
12-Nov-06	117.33[a]	12	263.92[b]	12					17.79
30-Jan-07	144.25[a]	12	224.90[b]	10					16.57
18-Mar-07	134.50[a]	11	239.50[b]	12					21.40
4-Apr-07, 15 to 45-cm shoots									
4-Apr-07, 1-m shoots									
11-May-07	151.75[a]	12	225.58[b]	12	187.25[a]	12			17.35
21-Jun-07	134.42[a]	12	241.33[b]	12	184.67[c]	12			12.85
24-Aug-07	154.75[a]	12	283.67[b]	12	194.83[c]	12			20.01
3-Dec-07	168.00[a]	12	231.08[b]	12	193.08[a]	12			12.22
14-Feb-08	150.45[a]	9	265.75[b]	7	214.78[c]	10			16.36
11-Apr-08	155.17[a]	12	219.00[b]	12	200.75[b]	12			14.42
9-May-08, 15 to 45-cm shoots									
9-May-08, 1-m shoots									
30-May-08	165.98[a]	11	267.75[b]	12	180.74[a]	11	240.58[b]	12	16.41

ANOVA statistics, including all ramet cohorts

Interaction, sampling date x ramet age

F (num df, denom df)	14.73 (18,392)
P	< 0.001

Table 3.7 (Continued)

	Ramet dry mass (kg)								
	2005[2]		2006		2007		2008		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
6-Sep-05	0.389	12							0.034
12-Nov-05	0.272	12							0.036
10-Jan-06	0.399	12							0.045
19-Mar-06	0.373	12							0.042
28-Apr-06, 15 to 45-cm shoots			0.039	12					0.003
28-Apr-06, 1-m shoots			0.051	12					0.003
26-May-06	0.584[a]	12	0.258[b]	12					0.048
1-Jul-06	0.423	12	0.451	12					0.044
6-Sep-06	0.561	12	0.512	12					0.107
12-Nov-06	0.600[a]	12	0.417[b]	12					0.105
30-Jan-07	0.515	11	0.473	11					0.068
18-Mar-07	0.436	12	0.521	12					0.070
4-Apr-07, 15 to 45-cm shoots					0.031	12			0.002
4-Apr-07, 1-m shoots					0.028	12			0.002
11-May-07	0.526[a]	12	0.436[b]	12	0.098[a]	12			0.067
21-Jun-07	0.440[a]	12	0.453[b]	12	0.226[a]	12			0.066
24-Aug-07	0.474[a]	12	0.517[b]	8	0.245[a]	12			0.065
3-Dec-07	0.626[a]	12	0.554[b]	12	0.307[a]	12			0.075
14-Feb-08	0.471[a]	8	0.677[a]	7	0.376[b]	11			0.152
11-Apr-08	0.478[a]	12	0.452[a]	12	0.316[b]	12			0.068
9-May-08, 15 to 45-cm shoots							0.030	12	0.003
9-May-08, 1-m shoots							0.049	10	0.006
30-May-08	0.583[a]	12	0.485[a]	12	0.279[b]	12	0.511[a]	9	0.069

ANOVA statistics, including all ramet cohorts

Interaction, sampling date x ramet age

F (num df, denom df)	4.48 (18,452)
P	< 0.001

Table 3.7 (Continued)

	Leaf dry mass (kg)						
	2005[2]		2006		2007		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
6-Sep-05	0.080	12					0.006
12-Nov-05	0.050	12					0.007
10-Jan-06	0.049	12					0.007
19-Mar-06	0.041	12					0.004
28-Apr-06, 15 to 45-cm shoots							
28-Apr-06, 1-m shoots							
26-May-06	0.155	12					0.013
1-Jul-06	0.083	12	0.055	12			0.012
6-Sep-06	0.123[a]	12	0.067[b]	12			0.035
12-Nov-06	0.108[a]	12	0.028[b]	12			0.025
30-Jan-07	0.062[a]	11	0.004[b]	11			0.010
18-Mar-07	0.032	12	0.001	12			0.009
4-Apr-07, 15 to 45-cm shoots							
4-Apr-07, 1-m shoots							
11-May-07	0.081[a]	12	0.025[b]	12			0.013
21-Jun-07	0.051	12	0.027	12	0.046	12	0.016
24-Aug-07	0.056	12	0.030	8	0.055	12	0.015
3-Dec-07	0.084[a]	12	0.034[b]	12	0.068[a]	12	0.023
14-Feb-08	0.045	8	0.046	7	0.061	11	0.023
11-Apr-08	0.024	12	0.003	12	0.027	12	0.008
9-May-08, 15 to 45-cm shoots							
9-May-08, 1-m shoots							
30-May-08	0.073[a]	12	0.020[b]	12	0.057[a]	12	0.012

ANOVA statistics, including all ramet cohorts

Interaction, sampling date x ramet age

F (num df, denom df)	4.32 (15,358)
P	< 0.001

Table 3.7 (Continued)

	Branch dry mass (kg)						
	2005[2]		2006		2007		SEM[3]
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
6-Sep-05	0.075	12					0.007
12-Nov-05	0.057	12					0.010
10-Jan-06	0.074	12					0.012
19-Mar-06	0.074	12					0.008
28-Apr-06, 15 to 45-cm shoots							
28-Apr-06, 1-m shoots							
26-May-06	0.122	12					0.013
1-Jul-06	0.086	12	0.065	12			0.009
6-Sep-06	0.105	12	0.076	12			0.020
12-Nov-06	0.126[a]	12	0.055[b]	12			0.020
30-Jan-07	0.108[a]	11	0.073[b]	11			0.012
18-Mar-07	0.080	12	0.068	12			0.013
4-Apr-07, 15 to 45-cm shoots							
4-Apr-07, 1-m shoots							
11-May-07	0.106[a]	12	0.073[b]	12			0.014
21-Jun-07	0.089[a]	12	0.064[ab]	12	0.039[b]	12	0.014
24-Aug-07	0.089[a]	12	0.052[b]	12	0.041[b]	12	0.012
3-Dec-07	0.129[a]	12	0.084[b]	12	0.062[b]	12	0.018
14-Feb-08	0.089	8	0.094	7	0.068	11	0.028
11-Apr-08	0.102[a]	12	0.076[ab]	12	0.065[b]	12	0.016
9-May-08, 15 to 45-cm shoots							
9-May-08, 1-m shoots							
30-May-08	0.109[a]	12	0.062[b]	12	0.063[b]	12	0.014

ANOVA statistics, including all ramet cohorts

Main effect of ramet age

F[4] (num df, denom df)	21.72 (3,362)
P[5]	< 0.001

Main effect of sampling date

F (num df, denom df)	3.70 (16,362)
P	< 0.001

Table 3.7 (Continued)

	Culm[5] dry mass (kg)						
	2005[2]		2006		2007		SEM
Sampling date	LS Mean[4]	N	LS Mean[4]	N	LS Mean[4]	N	
6-Sep-05	0.234	12					0.024
12-Nov-05	0.166	12					0.021
10-Jan-06	0.276	12					0.029
19-Mar-06	0.258	12					0.035
28-Apr-06, 15 to 45-cm shoots							
28-Apr-06, 1-m shoots							
26-May-06	0.307	12					0.030
1-Jul-06	0.253	12	0.332	12			0.028
6-Sep-06	0.333	12	0.369	12			0.056
12-Nov-06	0.366	12	0.335	12			0.062
30-Jan-07	0.344	11	0.396	11			0.049
18-Mar-07	0.324[a]	12	0.453[b]	12			0.051
4-Apr-07, 15 to 45-cm shoots							
4-Apr-07, 1-m shoots							
11-May-07	0.340	12	0.338	12			0.048
21-Jun-07	0.301[a]	12	0.362[a]	12	0.141[b]	12	0.039
24-Aug-07	0.330[a]	12	0.415[a]	12	0.149[b]	12	0.043
3-Dec-07	0.413[a]	12	0.436[a]	12	0.177[b]	12	0.048
14-Feb-08	0.337[a]	8	0.533[b]	7	0.246[a]	11	0.103
11-Apr-08	0.352[a]	12	0.373[a]	12	0.223[b]	12	0.051
9-May-08, 15 to 45-cm shoots							
9-May-08, 1-m shoots							
30-May-08	0.402[a]	12	0.403[a]	12	0.159[b]	12	0.046

ANOVA statistics, including all ramet cohorts

Interaction, sampling date x ramet age

F (num df, denom df)	7.33 (15,362)
P	< 0.001

[1]Residuals of the regression of measured ramet dry-matter biomass (kg) versus stem volume (ramet height x basal ramet diameter).
[2]Ramet cohort (year in which ramets emerged as shoots).
[3]Maximum standard error of the mean for compared least-square means
[4]Lettered superscripts indicate differences across rows ($P < 0.05$).
[5]Culm = central, woody stalk of bamboo
Notes: Data were collected at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2008. Least-square means are adjusted for other terms in the repeated-measures ANOVA model (PROC MIXED; SAS Institute 2012), with subplot as the repeated unit, testing for main effects and interaction of sampling date and ramet cohort.

Table 3.8 Biomass production and stand maturity by sampling date alone: *Phyllostachys aureosulcata*.

Sampling date	Production and recruitment parameters				Leaf dry mass (kg)					
	Live mature ramets/sq m		Asin (% live mature ramets)		2005[1]		2006		2007	
	LS Mean[2]	N	LS Mean[2]	N	LS Mean[2]	N	LS Mean[2]	N	LS Mean[2]	N
1-Jul-05	31.33^{ab}	12	1.112^{a}	12	0.059^{ab}	12				
6-Sep-05	23.33^{bcde}	12	1.074^{a}	12	0.069^{a}	12				
12-Nov-05	20.33^{cdef}	12	1.087^{a}	12	0.050^{abc}	12				
10-Jan-06	19.58^{cdef}	12	1.063^{a}	12	0.037^{bcde}	12				
19-Mar-06	17.50^{def}	12	1.054^{ab}	12	0.049^{abcd}	12				
26-May-06	17.67^{def}	12	0.77^{efg}	12	0.069^{a}	12				
1-Jul-06	33.67^{a}	12	1.02^{ab}	12	0.048^{abcd}	12	0.058^{cd}	12		
6-Sep-06	23.92^{abcde}	12	0.995^{abc}	12	0.042^{bcde}	12	0.085^{ab}	12		
12-Nov-06	16.75^{ef}	12	0.693^{fg}	12	0.051^{abc}	12	0.056^{cde}	12		
30-Jan-07	23.50^{bcde}	12	0.921^{bcd}	12	0.025^{cde}	11	0.031^{ef}	10		
18-Mar-07	24.92^{abcd}	12	0.882^{cde}	12	0.033^{bcde}	11	0.021^{f}	12		
11-May-07	31.33^{ab}	12	0.792^{def}	12	0.032^{cde}	12	0.041^{def}	12		
21-Jun-07	26.33^{abc}	12	0.751^{efg}	12	0.041^{bcde}	11	0.076^{bc}	12	0.034^{ab}	12
24-Aug-07	31.42^{ab}	12	0.858^{de}	12	0.035^{bcde}	12	0.109^{a}	12	0.046^{a}	12
3-Dec-07	27.67^{abc}	12	0.698^{fg}	12	0.028^{cde}	12	0.096^{ab}	12	0.013^{b}	12
14-Feb-08	29.30^{abc}	6	0.779^{defg}	6	0.018^{de}	6	0.041^{def}	6	0.015^{ab}	6
11-Apr-08	28.64^{abc}	6	0.718^{efg}	6	0.012^{e}	6	0.043^{def}	6	0.011^{b}	6
30-May-08	33.80^{a}	6	0.622^{gh}	6	0.031^{cde}	6	0.060^{cde}	6	0.016^{b}	6
SEM[3]	8.40		0.096		0.013		0.021		0.006	
F[4] (num df, den df)	7.85 (23,223)		24.37 (23,223)				3.75 (17,326)			
P[5]	< 0.001		< 0.001				< 0.001			

[1]Year in which ramets emerged.
[2]Lettered superscripts indicate differences within columns ($P < 0.05$)
[3]Maximum standard error of the mean for compared least-square means.
[4]F ratio (numerator degrees of freedom, denominator degrees of freedom) for 1-way (live ramets) or 2-way (leaf mass) repeated-measures Analysis of Variance of sampling-date effects.
[5]P-value for 1-way or 2-way repeated-measures ANOVA of sampling-date effects.
Notes: Measurements and samples were taken at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2008. Least-square means are adjusted for other terms in the repeated-measures ANOVA model (PROC MIXED; SAS Institute 2012), with subplot as the repeated unit.

Table 3.9 Biomass production and stand maturity by sampling date alone: *Phyllostachys glauca*.

Sampling date	Production and recruitment parameters				Leaf dry mass (kg)					
	Live mature ramets/sq m		Asin (% live mature ramets)		2005[1]		2006		2007	
	LS Mean[2]	N	LS Mean[2]	N	LS Mean[2]	N	LS Mean[2]	N	LS Mean[2]	N
6-Sep-05	9.50^{abc}	12	1.223^{ab}	12	0.124^{bc}	12				
12-Nov-05	16.42^{ef}	12	1.057^{cdef}	12	0.093^{cd}	12				
10-Jan-06	6.67^{ab}	12	1.203^{abc}	12	0.088^{cd}	12				
19-Mar-06	15.67^{def}	12	1.064^{bcdef}	12	0.058^{def}	12				
26-May-06	13.50^{cdef}	12	0.995^{efg}	12	0.205^{a}	12				
1-Jul-06	16.42^{ef}	12	1.263^{a}	12	0.141^{b}	12	0.098^{ab}	12		
6-Sep-06	16.42^{ef}	12	1.118^{abcde}	12	0.155^{b}	12	0.113^{a}	12		
12-Nov-06	16.42^{ef}	12	1.169^{abcd}	12	0.082^{cde}	12	0.069^{abcd}	12		
30-Jan-07	13.92^{cdef}	12	1.029^{def}	12	0.039^{ef}	11	0.027^{de}	9		
18-Mar-07	18.17^{fg}	12	1.053^{cdef}	12	0.030^{f}	12	0.002^{e}	12		
11-May-07	16.17^{efg}	12	0.845^{ghi}	12	0.070^{def}	12	0.065^{bcd}	12		
21-Jun-07	21.92^{g}	12	0.829^{hi}	12	0.091^{cd}	12	0.085^{abc}	12	0.068^{ab}	12
24-Aug-07	18.25^{fg}	12	1.059^{bcdef}	12	0.082^{cde}	11	0.096^{ab}	12	0.123^{a}	7
3-Dec-07	29.25^{h}	12	0.948^{fgh}	12	0.086^{cde}	12	0.069^{abcd}	12	0.045^{bc}	12
14-Feb-08	21.67^{g}	12	1.075^{bcdef}	12	0.043^{def}	9	0.047^{bcde}	9	0.027^{c}	8
11-Apr-08	19.08^{fg}	12	0.845^{ghi}	12	0.072^{def}	12	0.046^{cde}	12	0.028^{c}	12
30-May-08	17.25^{fg}	12	0.742^{ij}	12	0.068^{def}	12	0.106^{bcd}	12	0.076^{ab}	12
SEM[3]	3.49		0.134		0.041		0.031		0.024	
F[4] (num df, den df)	7.41 (22,257)		13.72 (22,257)				9.39 (16,354)			
P[5]	< 0.001		< 0.001				< 0.001			

[1]Year in which ramets emerged.
[2]Lettered superscripts indicate differences within columns ($P < 0.05$)
[3]Maximum standard error of the mean for compared least-square means.
[4]F ratio (numerator degrees of freedom, denominator degrees of freedom) for 1-way (live ramets) or 2-way (leaf mass) repeated-measures Analysis of Variance of sampling-date effects.
[5]P-value for 1-way or 2-way repeated-measures ANOVA of sampling-date effects.
Notes: Measurements and samples were taken at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2008. Least-square means are adjusted for other terms in the repeated-measures ANOVA model (PROC MIXED; SAS Institute 2012), with subplot as the repeated unit.

Table 3.10 Biomass production and stand maturity by sampling date alone: *Phyllostachys rubromarginata*.

Sampling date	Production and recruitment parameters				Leaf dry mass (kg)					
	Live mature ramets/sq m		Asin (% live mature ramets)		2005[1]		2006		2007	
	LS Mean[2]	N	LS Mean[2]	N	LS Mean[2]	N	LS Mean[2]	N	LS Mean[2]	N
6-Sep-05	17.78^{bcde}	12	1.330^{gh}	12	0.080^{defg}	12				
12-Nov-05	16.00^{bcd}	12	1.253^{g}	12	0.050^{abcd}	12				
10-Jan-06	12.04^{ab}	12	1.271^{g}	12	0.049^{abcd}	12				
19-Mar-06	13.92^{bc}	12	1.273^{g}	12	0.041^{abc}	12				
26-May-06	12.50^{abc}	12	0.961^{cde}	12	0.155^{i}	12				
1-Jul-06	22.50^{def}	12	1.486^{h}	12	0.083^{efg}	12	0.055^{ab}	12		
6-Sep-06	19.92^{cde}	12	1.321^{gh}	12	0.123^{hi}	12	0.067^{a}	12		
12-Nov-06	23.58^{efg}	12	1.331^{gh}	12	0.108^{gh}	12	0.028^{bcde}	12		
30-Jan-07	19.17^{bcde}	12	1.171^{fg}	12	0.062^{bcdef}	11	0.004^{de}	11		
18-Mar-07	21.69^{de}	12	1.265^{g}	12	0.032^{ab}	12	0.001^{e}	12		
11-May-07	25.42^{efgh}	12	0.907^{bcd}	12	0.081^{defg}	12	0.025^{bcde}	12		
21-Jun-07	21.83^{de}	12	0.882^{bc}	12	0.051^{abcde}	12	0.027^{bcde}	12	0.046^{ab}	12
24-Aug-07	31.75^{hi}	12	1.080^{ef}	12	0.056^{abcdef}	12	0.030^{bcde}	8	0.055^{ab}	12
3-Dec-07	30.08^{ghi}	12	0.944^{bcde}	12	0.084^{fg}	12	0.034^{bcd}	12	0.068^{b}	12
14-Feb-08	34.58^{i}	12	1.056^{def}	12	0.045^{abcd}	8	0.046^{abc}	7	0.061^{b}	11
11-Apr-08	29.58^{fghi}	12	0.916^{bcde}	12	0.024^{a}	12	0.003^{de}	12	0.027^{a}	12
30-May-08	24.25^{efg}	12	0.781^{b}	12	0.073^{cdef}	12	0.020^{cde}	12	0.057^{b}	12
SEM[3]	4.79		0.105		0.035		0.019		0.015	
F[4] (num df, den df)	9.33 (22,237)		22.34 (22,237)				9.43 (16,358)			
P[5]	< 0.001		< 0.001				< 0.001			

[1]Year in which ramets emerged.
[2]Lettered superscripts indicate differences within columns ($P < 0.05$)
[3]Maximum standard error of the mean for compared least-square means.
[4]F ratio (numerator degrees of freedom, denominator degrees of freedom) for 1-way (live ramets) or 2-way (leaf mass) repeated-measures Analysis of Variance of sampling-date effects.
[5]P-value for 1-way or 2-way repeated-measures ANOVA of sampling-date effects.
Notes: Measurements and samples were taken at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2008. Least-square means are adjusted for other terms in the repeated-measures ANOVA model (PROC MIXED; SAS Institute 2012), with subplot as the repeated unit.

Table 3.11 Correlation analyses of weather conditions.

Variable	Correlation		
	r	N	*P*
Mean monthly temperature			
Ramet dry mass	0.051	1487	0.05
Ramet height	0.114	1479	< 0.001
Height of lowest branch	0.081	1251	< 0.01
Basal culm[1] diameter	0.121	1435	< 0.001
Dry mass of leaves	0.220	1177	< 0.001
Asin (% live mature ramets)	0.054	1533	0.04
Total monthly precipitation			
Residual biomass[2]	-0.166	1411	< 0.001
Ramet dry mass	-0.107	1487	< 0.001
Ramet height	-0.197	1479	< 0.001
Basal culm[1] diameter	0.056	1435	0.03
Dry mass of branches	0.067	1187	0.02
Asin (% live mature ramets)	-0.232	1533	< 0.001

[1]Central woody stem of bamboo.
[2]Residuals of the regression of measured ramet dry-matter biomass (kg) versus stem volume (ramet height x basal ramet diameter), an index of expected biomass.
Notes: Weather data for the months encompassing the study period (July 2005 and July 2008) were taken from a NOAA weather station located at Shelby County AgriCenter, Memphis, Tennessee, USA (35° 7'47"N, 89°48'13"W), 2.5 km from the study site. Weather and biomass data from *Phyllostachys aureosulcata, P. glauca,* and *P. rubromarginata* were compared using simple linear correlation (PROC CORR; SAS Institute 2012).

Table 3.12 Recruitment and mortality by disturbance treatment and study year

Disturbance treatment[1]	Live shoots per sq m								Arcsine (percent live shoots)							
	Year 1[2]		Year 2		Year 3		ANOVA statistics		Year 1		Year 2		Year 3		ANOVA statistics	
	Mean[3]	N	Mean	N	Mean	N	F (num df, den df)	*P*	Mean	N	Mean	N	Mean	N	F (num df, den df)	*P*
PLLAU[4]																
Control	6.75	4	7.75	4	10.50	4			0.471	4	0.357	4	0.377	4		
3%	12.25	4	11.50	4	15.00	4			0.596[1]	4	0.443[12]	4	0.338[2]	4		
20%	10.75	2	11.75	2	17.00	2			0.707[1]	2	0.436[2]	2	0.478[12]	2		
SEM[5]	2.50		4.52		7.50				0.176		0.086		0.086			
Interaction							0.08 (4,21)	0.99							0.60 (4,21)	0.67
Treatment ME[6]							1.81 (2,21)	0.19							2.43 (2,21)	0.11
Study Year ME							1.08 (2,21)	0.36							6.81 (2,21)	< 0.01
PLLGL[4]																
Control	4.75	4	3.75	4	4.25	4			0.471	4	0.342	4	0.315	4		
3%	3.75	4	5.50	4	5.50	4			0.551	4	0.420	4	0.353	4		
20%	3.50	4	5.75	4	5.50	4			0.415	4	0.489	4	0.327	4		
SEM	1.38		2.17		3.23				0.131		0.084		0.128			
Interaction							0.22 (4,27)	0.92							0.52 (4,27)	0.72
Treatment ME							0.28 (2,27)	0.75							2.37 (2,27)	0.11
Study Year ME							0.12 (2,27)	0.89							0.46 (2,27)	0.64
PLLRU[4]																
Control	4.00[1]	4	8.25[2]	4	5.25[12]	4			0.581[a1]	4	0.441[a12]	4	0.285[a2]	4		
3%	4.75[1]	4	10.50[2]	4	4.50[1]	4			0.623[a1]	4	0.561[a1]	4	0.331[a2]	4		
20%	2.75[1]	4	9.00[2]	4	7.50[2]	4			0.325[b1]	4	0.552[a2]	4	0.378[a12]	4		
SEM	1.38		1.70		2.46				0.105		0.065		0.087			
Interaction							0.93 (4,27)	0.46							2.83 (4,27)	0.04
Treatment ME							0.20 (2,27)	0.82								
Study Year ME							9.78 (2,27)	< 0.001								

Table 3.12 (Continued)

Disturbance treatment[1]	Live mature ramets per sq m								Arcsine (percent live mature ramets)							
	Year 1[2]		Year 2		Year 3		ANOVA statistics		Year 1		Year 2		Year 3		ANOVA statistics	
	Mean[3]	N	Mean	N	Mean	N	F (num df, den df)	*P*	Mean	N	Mean	N	Mean	N	F (num df, den df)	*P*
PLLAU[4]																
Control	22.00	4	37.75	4	20.50	4			0.916	4	0.796	4	0.584	4		
3%	16.75[1]	4	30.75[12]	4	45.50[2]	4			0.708	4	0.814	4	0.605	4		
20%	14.25[1]	2	25.50[2]	2	37.50[12]	2			0.691	2	0.764	2	0.748	2		
SEM[5]	8.25		11.29		17.32				0.114		0.085		0.160			
Interaction							1.19 (4,21)	0.34							1.46 (4,21)	0.25
Treatment ME[6]							0.36 (2,21)	0.70							0.32 (2,21)	0.73
Study Year ME							4.07 (2,21)	0.03							2.07 (2,21)	0.15
PLLGL[4]																
Control	15.75	4	17.50	4	22.75	4			0.980[1]	4	0.922[12]	4	0.789[2]	4		
3%	10.50	4	19.25	4	11.75	4			1.000[1]	4	0.823[12]	4	0.721[2]	4		
20%	14.25	4	11.75	4	17.25	4			1.005[1]	4	0.789[2]	4	0.718[2]	4		
SEM	5.46		10.58		9.61				0.131		0.084		0.128			
Interaction							1.12 (4,27)	0.37							0.42 (4,27)	0.79
Treatment ME							0.78 (2,27)	0.47							0.72 (2,27)	0.49
Study Year ME							1.45 (2,27)	0.25							11.55 (2,27)	< 0.001
PLLRU[4]																
Control	9.25[1]	4	30.00[2]	4	28.50[2]	4			0.948	4	0.924	4	0.808	4		
3%	6.25[1]	4	22.75[2]	4	17.00[12]	4			0.768	4	0.886	4	0.746	4		
20%	22.00	4	23.50	4	27.25	4			1.168[1]	4	0.911[2]	4	0.791[2]	4		
SEM	3.24		7.94		5.06				0.130		0.092		0.077			
Interaction							1.26 (4,27)	0.31							1.66 (4,27)	0.19
Treatment ME							2.93 (2,27)	0.07							2.72 (2,27)	0.08
Study Year ME							6.65 (2,27)	< 0.01							3.71 (2,27)	0.04

Table 3.12 (Continued)

Disturbance treatment[1]	Dead mature ramets per sq m								Arcsine (percent dead mature ramets)							
	Year 1[2]		Year 2		Year 3		ANOVA statistics		Year 1		Year 2		Year 3		ANOVA statistics	
	Mean[3]	N	Mean	N	Mean	N	F (num df, den df)	*P*	Mean	N	Mean	N	Mean	N	F (num df, den df)	*P*
PLLAU[4]																
Control	6.75[1]	4	12.00[12]	4	22.00[2]	4			0.404	4	0.476	4	0.644	4		
3%	7.00[1]	4	7.25[1]	4	18.50[2]	4			0.482	4	0.402	4	0.554	4		
20%	14.50	4	12.25	4	16.25	4			0.491	4	0.481	4	0.588	4		
SEM[5]	5.97		3.15		7.14				0.101		0.144		0.088			
Interaction							0.84 (4,27)	0.51							0.38 (4,27)	0.82
Treatment ME[6]							0.62 (2,27)	0.55							0.20 (2,27)	0.82
Study Year ME							5.21 (2,27)	0.01							3.00 (2,27)	0.07
PLLGL[4]																
Control			2.75[1]	4	11.50[2]	4					0.281[1]	4	0.560[2]	4		
3%			3.25[1]	4	12.00[2]	4					0.320[1]	4	0.669[2]	4		
20%			0.00[1]	4	12.00[2]	4					0.000[1]	4	0.598[2]	4		
SEM			1.80		2.02						0.129		0.065			
Interaction							0.73 (2,18)	0.50							2.27 (2,18)	0.13
Treatment ME							0.57 (2,18)	0.57							3.13 (2,18)	0.07
Study Year ME							59.85 (1,18)	< 0.001							40.38 (1,18)	< 0.001
PLLRU[4]																
Control			0.00[1]	4	3.75[2]	4					0.000	4	0.244	4		
3%			0.25[1]	4	4.25[2]	4					0.051	4	0.319	4		
20%			0.50[1]	4	8.00[2]	4					0.058	4	0.455	4		
SEM			0.50		2.32						0.058		0.128			
Interaction							1.24 (2,18)	0.31							0.62 (2,18)	0.55
Treatment ME							1.84 (2,18)	0.19							1.64 (2,18)	0.22
Study Year ME							21.93 (1,18)	< 0.001							24.95 (1,18)	< 0.001

Table 3.12 (Continued)

Disturbance treatment[1]	Dead shoots per sq m							Arcsine (percent dead shoots)						
	Year 1[2]		Year 2		Year 3		ANOVA statistics	Year 1		Year 2		Year 3		ANOVA statistics
	Mean[3]	N	Mean	N	Mean	N	F (num df, den df) *P*	Mean	N	Mean	N	Mean	N	F (num df, den df) *P*
PLLAU[4]														
Control			2.00	4	4.25	4				0.154	4	0.247	4	
3%			2.00	4	1.25	4				0.258	4	0.125	4	
20%			3.25	4	4.00	4				0.246	4	0.274	4	
SEM[5]			1.08		1.89					0.136		0.072		
Interaction							0.88 (2,18) 0.43							1.24 (2,18) 0.31
Treatment ME[6]							1.69 (2,18) 0.21							0.50 (2,18) 0.61
Study Year ME							0.66 (1,18) 0.43							0.004 (1,18) 0.95
PLLGL[4]														
Control			0.50	4	0.50	4				0.080	4	0.078	4	
3%			0.25	4	0.25	4				0.077	4	0.048	4	
20%			3.00	4	0.25	4				0.202	4	0.036	4	
SEM			3.00		0.29					0.080		0.048		
Interaction							0.79 (2,18) 0.47							0.40 (2,18) 0.68
Treatment ME							0.68 (2,18) 0.52							0.17 (2,18) 0.84
Study Year ME							0.79 (1,18) 0.38							0.65 (1,18) 0.43
PLLRU[4]														
Control			0.25	4	1.75	4				0.054	4	0.204	4	
3%			0.00	4	0.75	4				0.000	4	0.136	4	
20%			0.75	4	0.00	4				0.092	4	0.000	4	
SEM			0.75		0.63					0.092		0.080		
Interaction							3.15 (2,18) 0.07							2.42 (2,18) 0.12
Treatment ME														0.96 (2,18) 0.40
Study Year ME														1.64 (1,18) 0.22

Table 3.12 (Continued)

Disturbance treatment[1]	Total dead ramets per sq m								Arcsine (percent total dead ramets)							
	Year 1[2]		Year 2		Year 3		ANOVA statistics		Year 1		Year 2		Year 3		ANOVA statistics	
	Mean[3]	N	Mean	N	Mean	N	F (num df, den df)	*P*	Mean	N	Mean	N	Mean	N	F (num df, den df)	*P*
PLLAU[4]																
Control			14.00[1]		26.25[2]						0.516[1]		0.719[2]			
3%			9.25		19.75						0.583		0.591			
20%			15.50		20.25						0.552		0.667			
SEM[5]			3.93		6.66						0.063		0.077			
Interaction							0.49 (2,18)	0.62							1.47 (2,18)	0.26
Treatment ME[6]							1.01 (2,18)	0.38							0.15 (2,18)	0.86
Study Year ME							7.97 (1,18)	0.01							5.52 (1,18)	0.03
PLLGL[4]																
Control			3.25[1]		12.00[2]						0.324		0.574			
3%			3.50[1]		12.25[2]						0.396		0.678			
20%			3.00[1]		12.25[2]						0.202[1]		0.604[2]			
SEM			1.70		1.91						0.202		0.064			
Interaction							0.01 (2,18)	0.99							0.29 (2,18)	0.75
Treatment ME							0.01 (2,18)	0.99							0.83 (2,18)	0.45
Study Year ME							31.66 (1,18)	< 0.001							40.38 (1,18)	< 0.001
PLLRU[4]																
Control			0.25[1]		5.50[2]						0.054[1]		0.377[2]			
3%			0.25[1]		5.00[2]						0.051[1]		0.369[2]			
20%			1.25[1]		8.00[2]						0.150[1]		0.455[2]			
SEM			0.75		2.38						0.091		0.141			
Interaction							0.31 (2,18)	0.74							0.01 (2,18)	0.99
Treatment ME							1.37 (2,18)	0.28							0.88 (2,18)	0.43
Study Year ME							26.88 (1,18)	< 0.001							24.44 (1,18)	< 0.001

[1]Aboveground disturbance treatments (administered quarterly) are as follows: control (no bamboo removal), 3% annual removal of live individual ramets, and 20% annual removal.

[2]Year 1 = 2006; Year 2 = 2007; Year 3 = 2008

[3]Lettered superscripts indicate differences among means within columns; numbered superscripts indicate differences among means across rows.

[4]PLLAU = *Phyllostachys aureosulcata*; PLLGL = *P. glauca*; PLLRU = *P. rubromarginata.*

[5]Maximum standard error of the mean for disturbance-treatment effects, by study year.

[6]Main effect

Notes: Measurements were made at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2008. Significance level of $\alpha = 0.05$ used for all comparisons among means (PROC GLM; SAS Institute 2012).

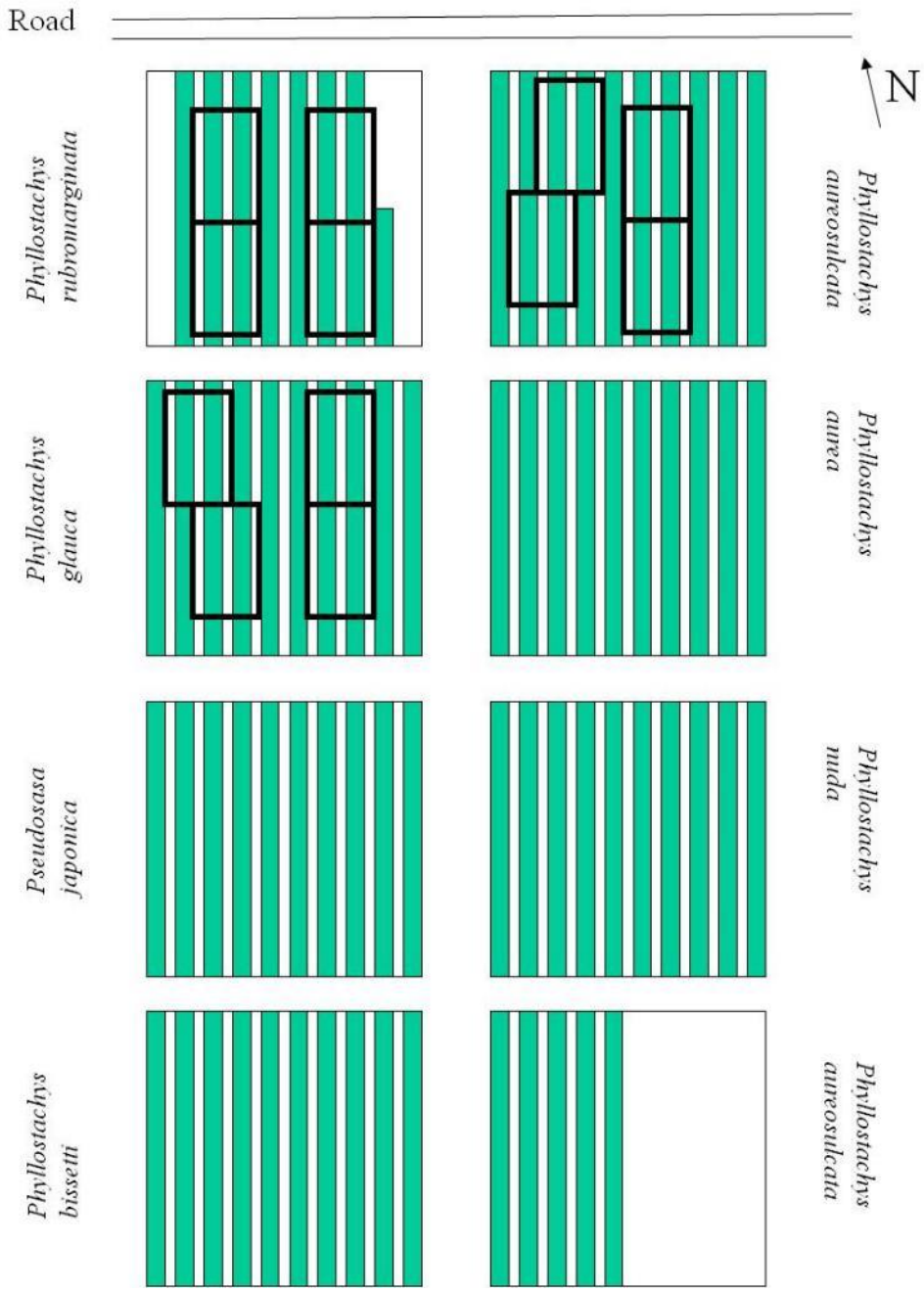

Figure 3.1 Schematic of research plots: Overall layout.

Memphis Zoo-operated browse farm at Shelby County AgriCenter, Memphis, TN. Eight 0.4-ha monoculture plots were planted with 7 bamboo species in 10 rows per plot. Bamboo growth is indicated by green-shaded areas, with mowed aisles (in white) between each row. Experimental enclosures are indicated with black rectangles within each of 3 bamboo species.

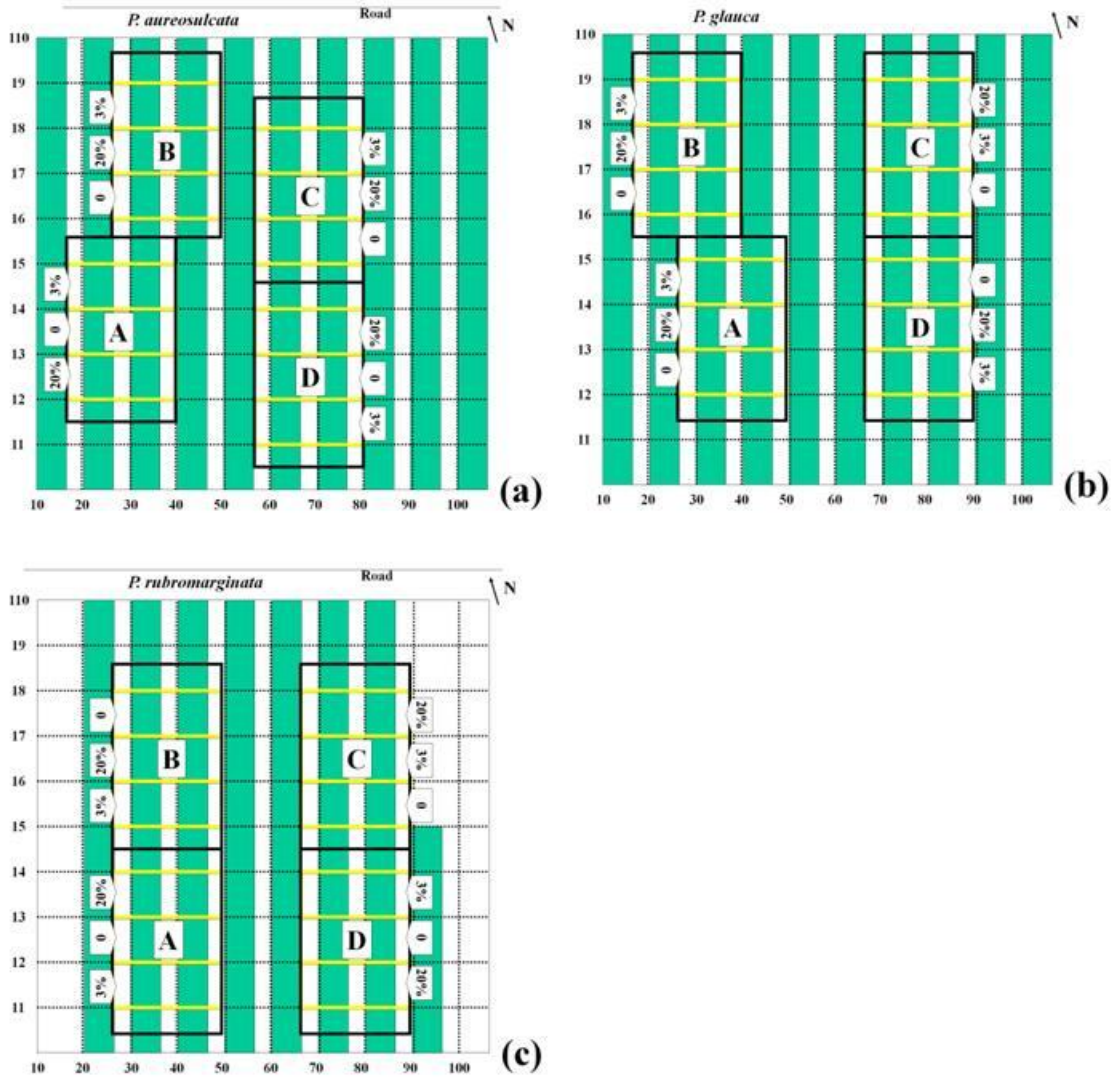

Figure 3.2 Schematic of research plots: Individual bamboo plots.

(a) *Phyllostachys aureosulcata*
(b) *Phyllostachys glauca*
(c) *Phyllostachys rubromarginata*

Within each monoculture plot, a sampling grid (10 x 10, 6-m line spacing) was established (indicated by dashed lines), with numbered flags at intersections to mark location. Replicate enclosures are indicated by black rectangles and letters, and subplots are indicated in yellow. Three disturbance treatments were randomly applied to each enclosure (1 treatment/subplot), and are indicated to the side of each suplot: control (0 bamboo removal), 3% annual removal of live ramets, and 20% annual removal.

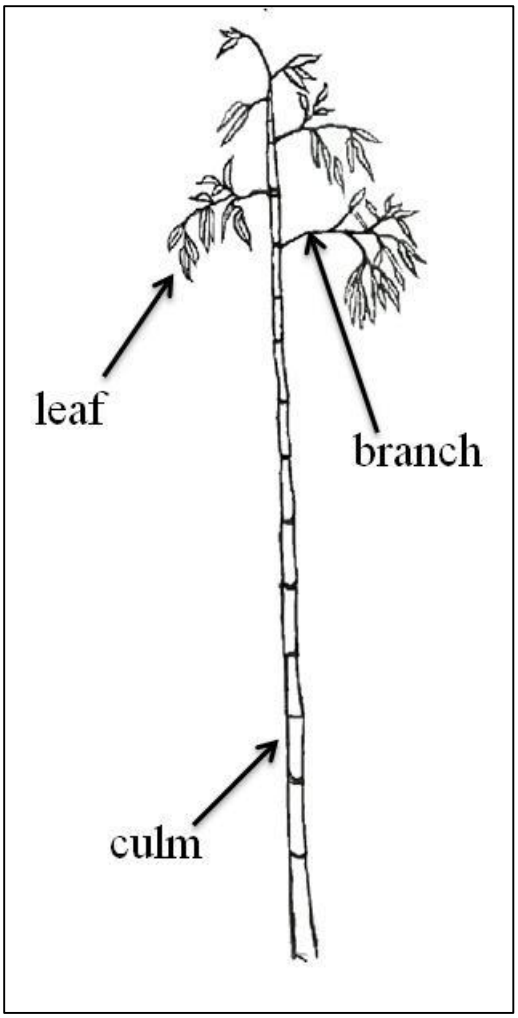

Figure 3.3 Anatomical divisions of *Phyllostachys* bamboo.

Culm is the central support of each ramet, arising directly from a belowground rhizome and divided into hollow cells sectioned off by nodes (horizontal marks). Branches project laterally from nodes, and leaves grow on the distal half of branches.

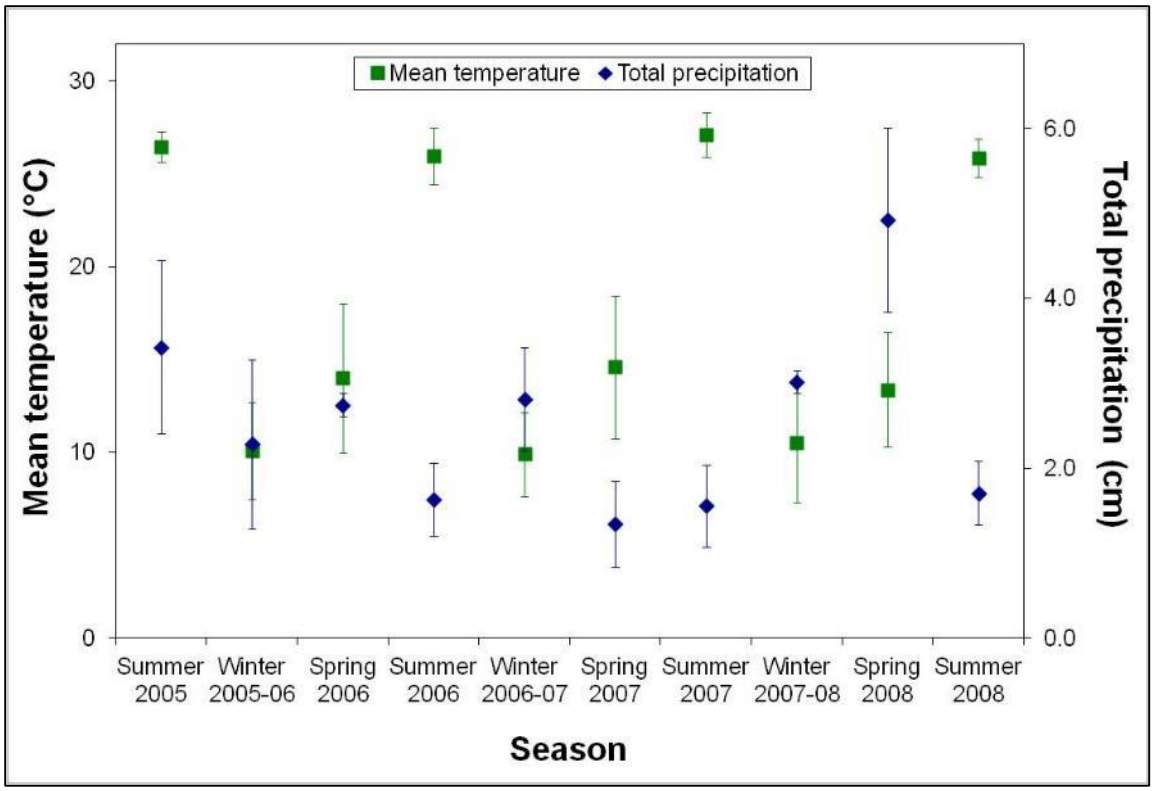

Figure 3.4 Weather data for study period.

Data are taken from a NOAA weather station located at Shelby County AgriCenter, Memphis, Tennessee, USA (35° 7'47"N, 89°48'13"W), 2.5 kilometers from the study site. Mean monthly temperature and total monthly precipitation are averaged by season (Spring = February through May; Summer = June through September; Winter = October through January). Bars indicate standard error.

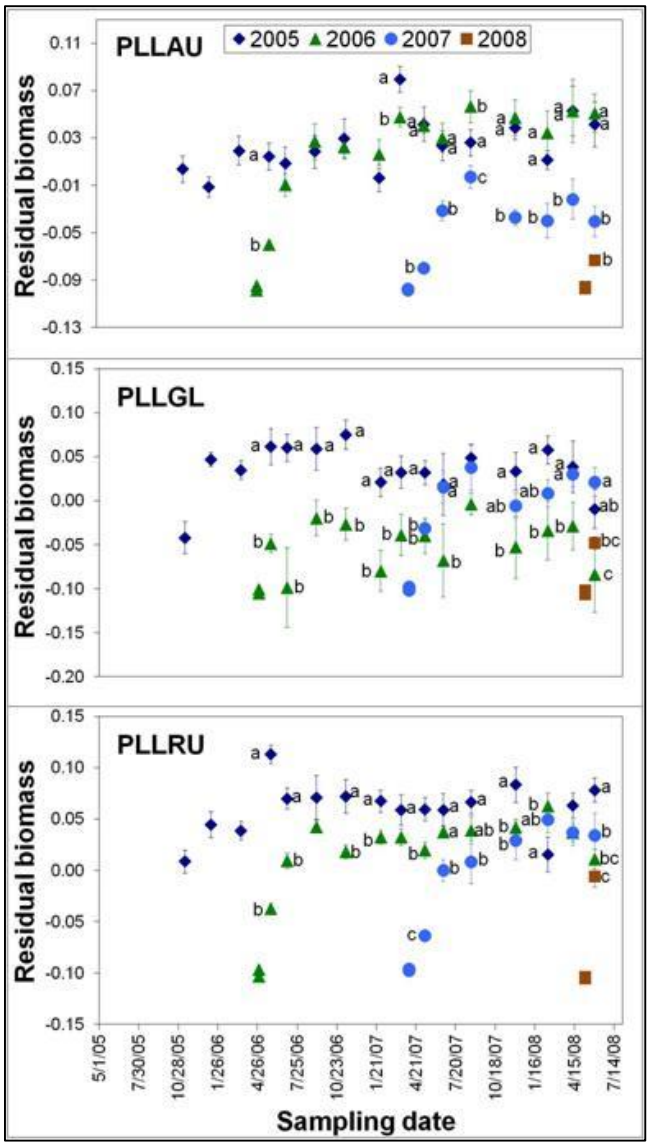

Figure 3.5 Residual biomass by ramet cohort and sampling date.

Lettered superscripts indicate differences among cohorts ($P < 0.05$) at a given sampling date; bars indicate standard error. Data were collected at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2008. Residual biomass was calculated by regressing measured ramet dry-matter biomass (kg) against stem volume [(ramet height) x (basal ramet diameter)] and determining the residuals of that relationship. Least-square means are adjusted for other terms in a mixed-model repeated-measures ANOVA (PROC MIXED; SAS Institute 2012), with subplot as the repeated unit, testing for main effects and interaction of sampling date and ramet age. Each data series represents a cohort of ramets that emerged as shoots in the year indicated. PLLAU = *Phyllostachys aureosulcata*; PLLGL = *P. glauca*; PLLRU = *P. rubromarginata*.

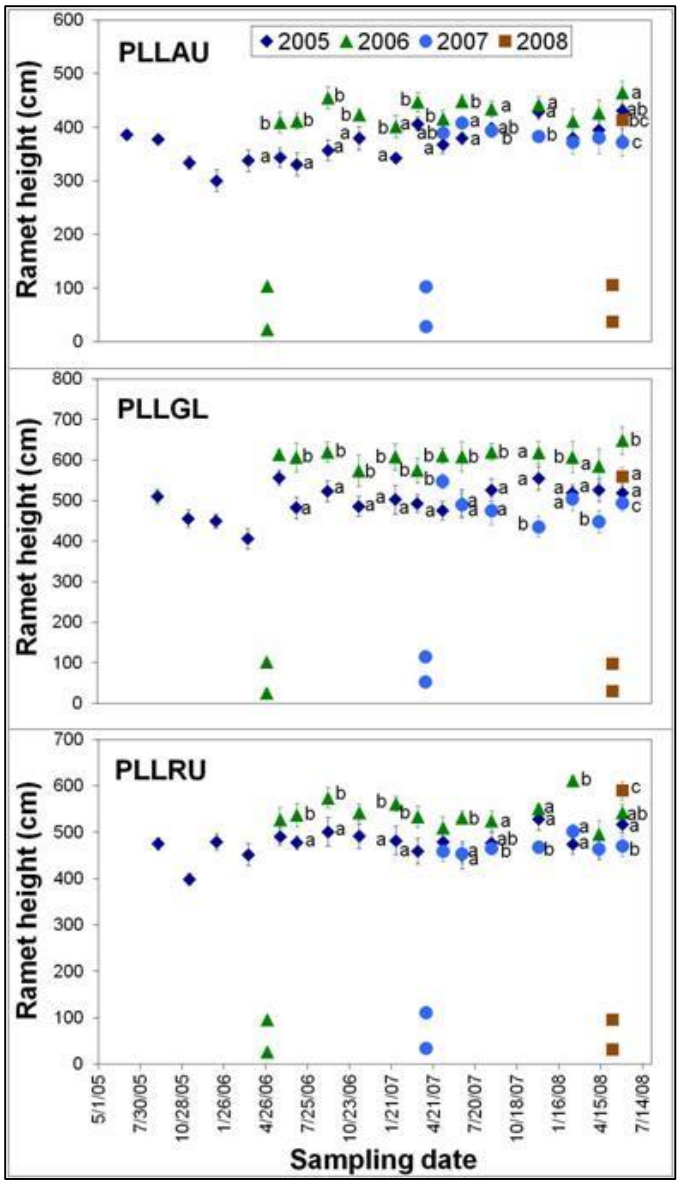

Figure 3.6 Ramet height by ramet cohort and sampling date.

Lettered superscripts indicate differences among cohorts ($P < 0.05$) at a given sampling date; bars indicate standard error. Data were collected at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2008. Least-square means are adjusted for other terms in a mixed-model repeated-measures ANOVA (PROC MIXED; SAS Institute 2012), with subplot as the repeated unit, testing for main effects and interaction of sampling date and ramet age. Each data series represents a cohort of ramets that emerged as shoots in the year indicated. PLLAU = *Phyllostachys aureosulcata*; PLLGL = *P. glauca*; PLLRU = *P. rubromarginata*.

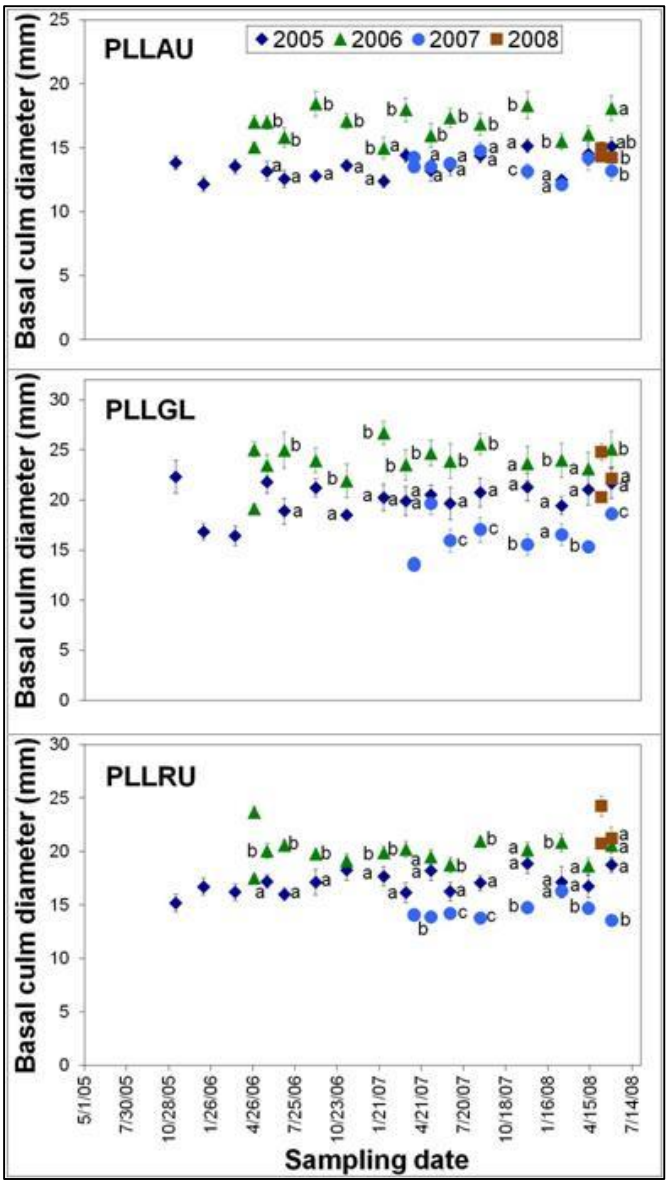

Figure 3.7 Basal culm diameter by ramet cohort and sampling date.

Lettered superscripts indicate differences among cohorts ($P < 0.05$) at a given sampling date; bars indicate standard error. Data were collected at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2008. Least-square means are adjusted for other terms in a mixed-model repeated-measures ANOVA (PROC MIXED; SAS Institute 2012), with subplot as the repeated unit, testing for main effects and interaction of sampling date and ramet age. Each data series represents a cohort of ramets that emerged as shoots in the year indicated. PLLAU = *Phyllostachys aureosulcata*; PLLGL = *P. glauca*; PLLRU = *P. rubromarginata*.

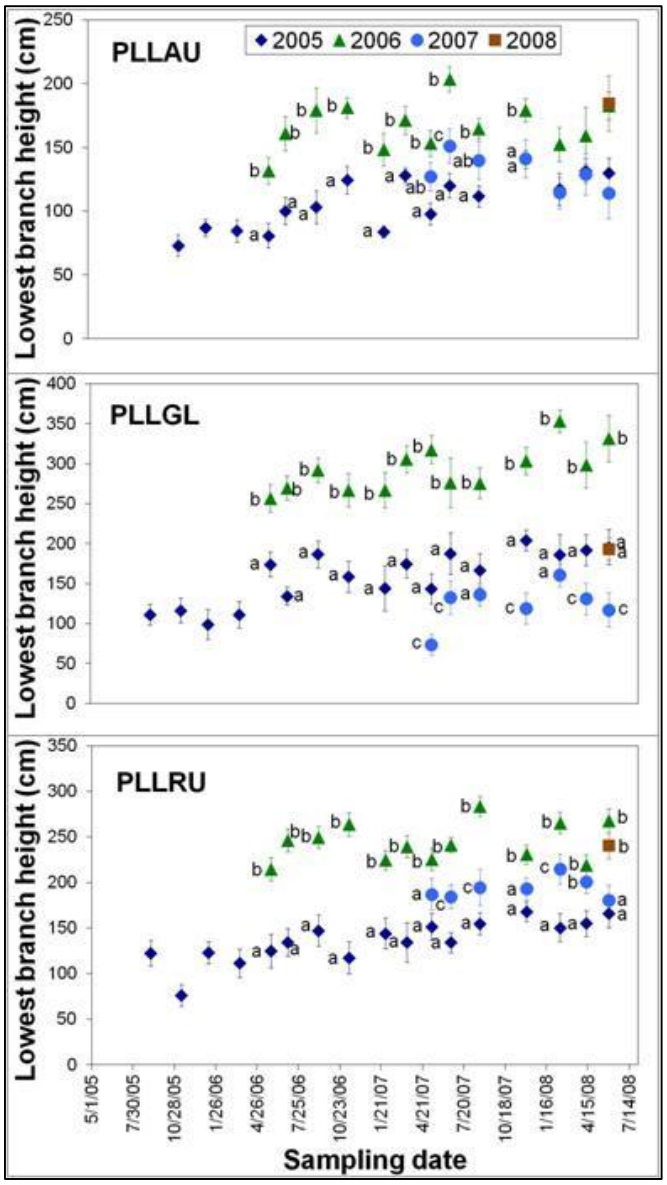

Figure 3.8 Lowest branch height by ramet cohort and sampling date.

Lettered superscripts indicate differences among cohorts ($P < 0.05$) at a given sampling date; bars indicate standard error. Data were collected at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2008. Least-square means are adjusted for other terms in a mixed-model repeated-measures ANOVA (PROC MIXED; SAS Institute 2012), with subplot as the repeated unit, testing for main effects and interaction of sampling date and ramet age. Each data series represents a cohort of ramets that emerged as shoots in the year indicated. PLLAU = *Phyllostachys aureosulcata*; PLLGL = *P. glauca*; PLLRU = *P. rubromarginata*.

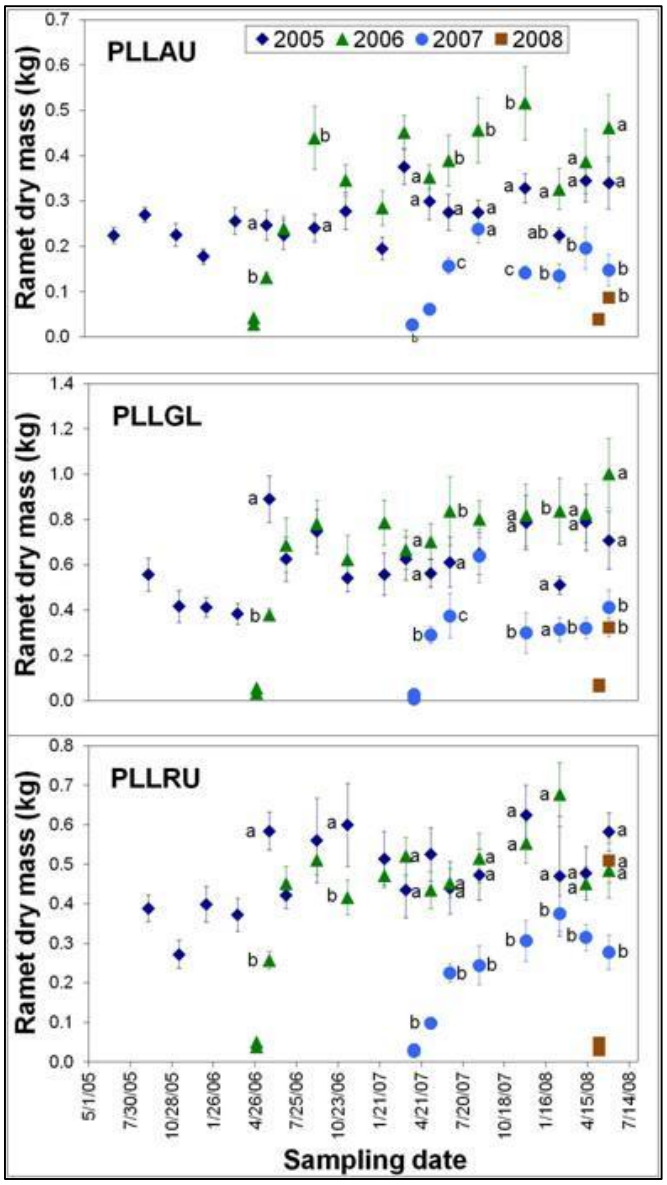

Figure 3.9 Total ramet dry mass by ramet cohort and sampling date.

Lettered superscripts indicate differences among cohorts ($P < 0.05$) at a given sampling date; bars indicate standard error. Data were collected at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2008. Least-square means are adjusted for other terms in a mixed-model repeated-measures ANOVA (PROC MIXED; SAS Institute 2012), with subplot as the repeated unit, testing for main effects and interaction of sampling date and ramet age. Each data series represents a cohort of ramets that emerged as shoots in the year indicated. PLLAU = *Phyllostachys aureosulcata*; PLLGL = *P. glauca*; PLLRU = *P. rubromarginata*.

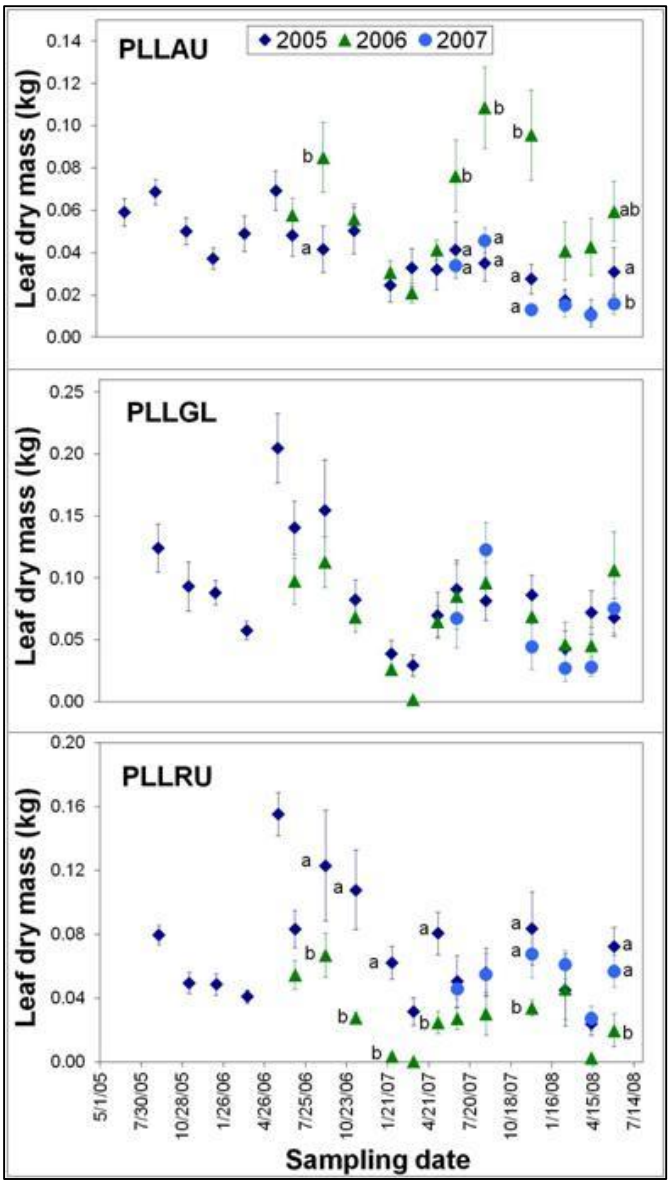

Figure 3.10 Dry mass of leaves by ramet cohort and sampling date.

Lettered superscripts indicate differences among cohorts ($P < 0.05$) at a given sampling date; bars indicate standard error. Data were collected at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2008. Least-square means are adjusted for other terms in a mixed-model repeated-measures ANOVA (PROC MIXED; SAS Institute 2012), with subplot as the repeated unit, testing for main effects and interaction of sampling date and ramet age. Each data series represents a cohort of ramets that emerged as shoots in the year indicated. PLLAU = *Phyllostachys aureosulcata*; PLLGL = *P. glauca*; PLLRU = *P. rubromarginata*.

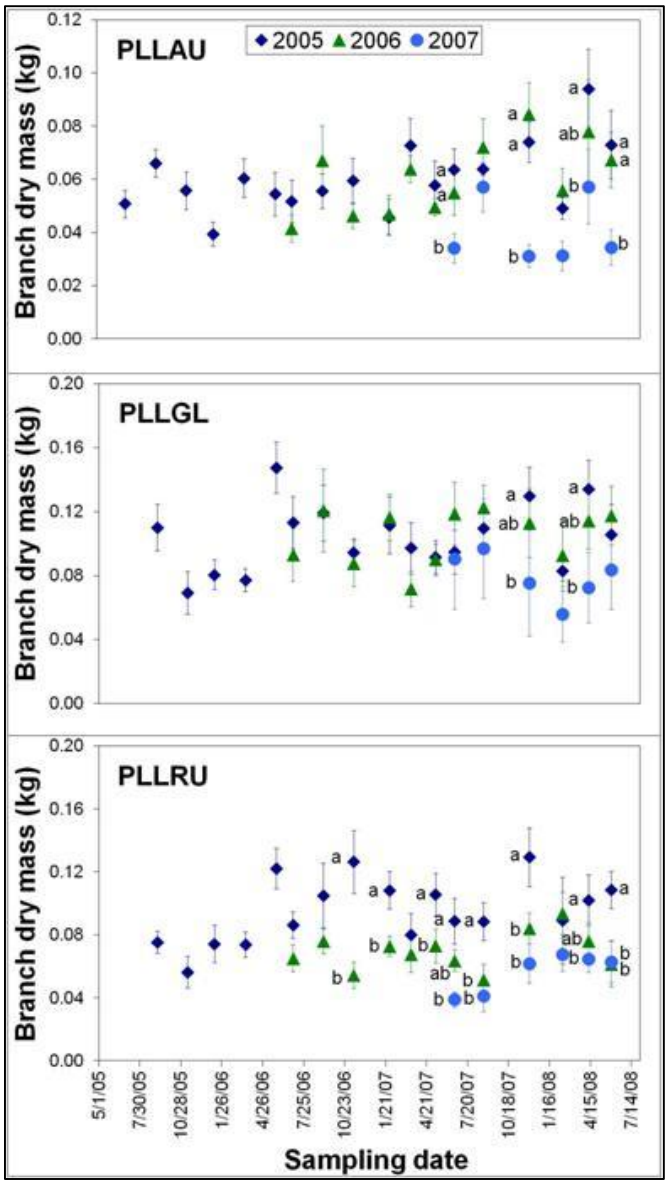

Figure 3.11 Dry mass of branches by ramet cohort and sampling date.

Lettered superscripts indicate differences among cohorts ($P < 0.05$) at a given sampling date; bars indicate standard error. Data were collected at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2008. Least-square means are adjusted for other terms in a mixed-model repeated-measures ANOVA (PROC MIXED; SAS Institute 2012), with subplot as the repeated unit, testing for main effects and interaction of sampling date and ramet age. Each data series represents a cohort of ramets that emerged as shoots in the year indicated. PLLAU = *Phyllostachys aureosulcata*; PLLGL = *P. glauca*; PLLRU = *P. rubromarginata*.

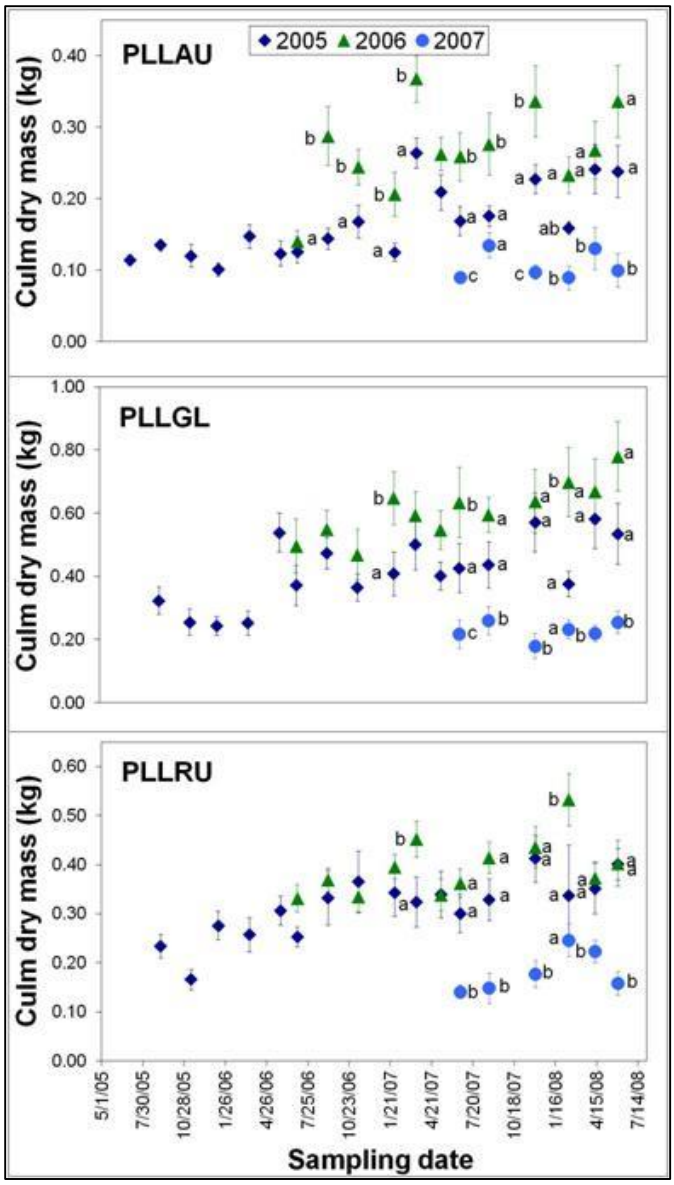

Figure 3.12 Dry mass of culms by ramet cohort and sampling date.

Lettered superscripts indicate differences among cohorts ($P < 0.05$) at a given sampling date; bars indicate standard error. Data were collected at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2008. Least-square means are adjusted for other terms in a mixed-model repeated-measures ANOVA (PROC MIXED; SAS Institute 2012), with subplot as the repeated unit, testing for main effects and interaction of sampling date and ramet age. Each data series represents a cohort of ramets that emerged as shoots in the year indicated. PLLAU = *Phyllostachys aureosulcata*; PLLGL = *P. glauca*; PLLRU = *P. rubromarginata*.

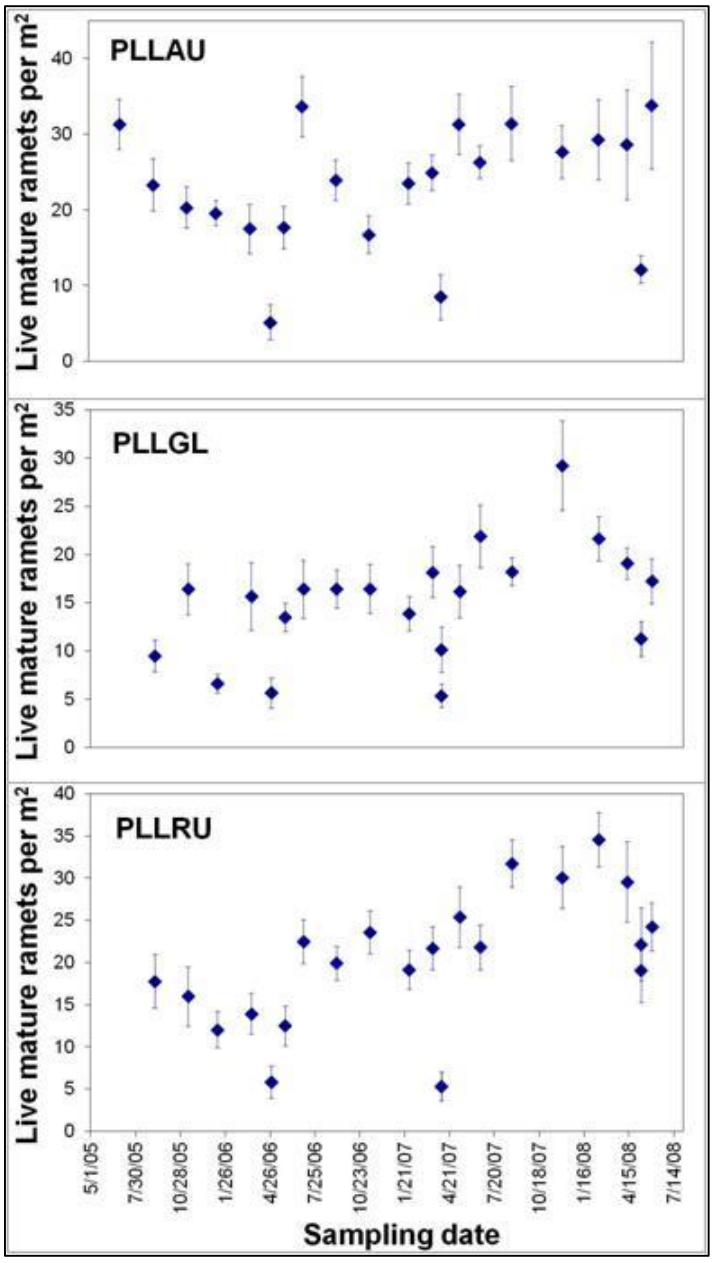

Figure 3.13 Density of live mature ramets by sampling date only.

Bars indicate standard error. Data were collected at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2008. Least-square means are adjusted for other terms in the 1-way repeated-measures ANOVA model (PROC MIXED; SAS Institute 2012), with subplot as the repeated unit. PLLAU = *Phyllostachys aureosulcata*; PLLGL = *P. glauca*; PLLRU = *P. rubromarginata*.

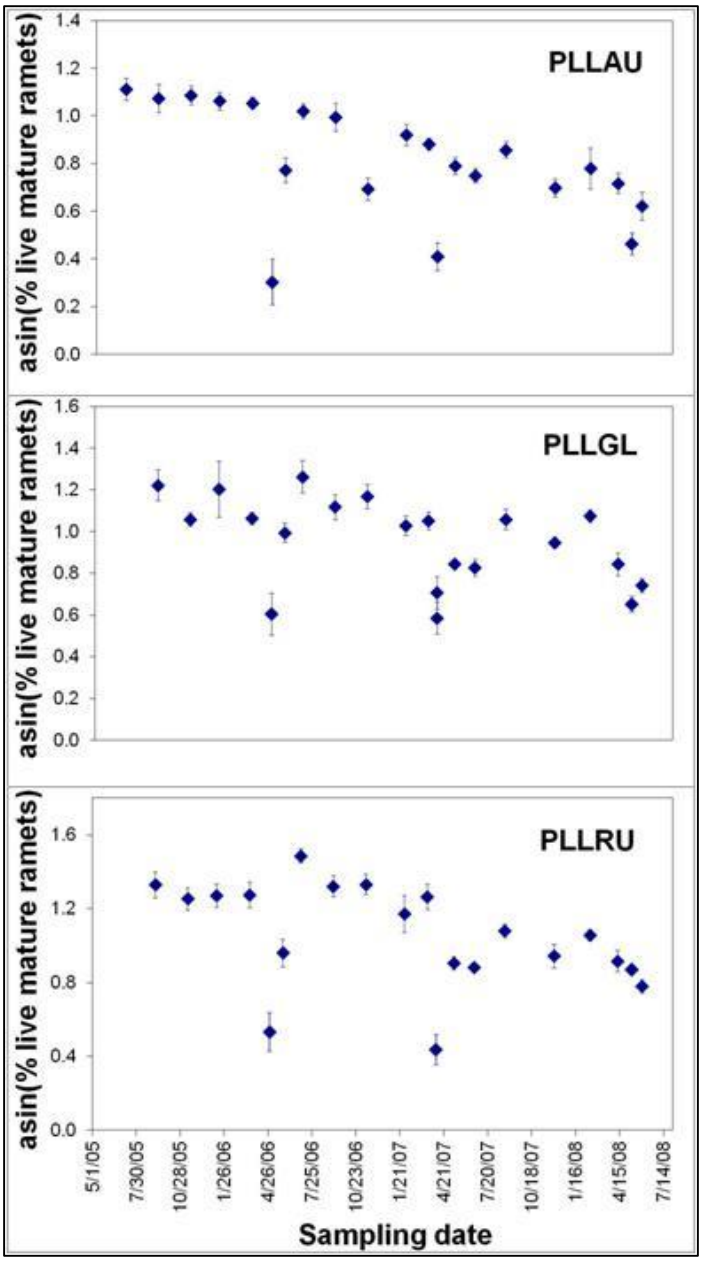

Figure 3.14 Proportion of live mature ramets by sampling date only.

Bars indicate standard error. Data were collected at the Shelby County AgriCenter, Memphis, Tennessee, USA, between July 2005 and July 2008. Least-square means are adjusted for other terms in the 1-way repeated-measures ANOVA model (PROC MIXED; SAS Institute 2012), with subplot as the repeated unit. PLLAU = *Phyllostachys aureosulcata*; PLLGL = *P. glauca*; PLLRU = *P. rubromarginata*.

CHAPTER IV

IMPACT OF SEASON AND BAMBOO DISTURBANCE ON GIANT PANDA FEEDING BEHAVIOR

Abstract

The giant panda is an herbivorous Carnivore, consuming fibrous bamboo but lacking gastrointestinal modifications for plant fiber digestion. To compensate, pandas display extreme dietary selectivity. Plant-part selection in particular is highly seasonal, although the reasons for seasonal differences are unknown. Wild and captive giant pandas live in very disturbed habitats, and the effects of disturbance on palatability of bamboo have not been studied. We tested whether bamboo selection by giant pandas changed by season and bamboo disturbance, and what biochemical changes in bamboo might drive those choices. We conducted 9 diet selection trials over 2.5 years, comparing diet selection for highly-disturbed versus less-disturbed *Phyllostachys aureosulcata*, and analyzing bamboo samples for allelochemicals, silica, and starches. We confirmed seasonal patterns in plant-part selection, but did not detect previously-reported correlations between leaf consumption and silica. Culm (stem) starch analyses were insufficient to establish a clear annual pattern, and we recommend further investigation of non-structural carbohydrates, a significant source of energy for pandas. We failed to detect a change in diet selection of bamboo by disturbance treatment, nor did we detect allelochemicals in any samples analyzed. We postulate that 1) bamboo palatability may

not change under disturbance, 2) disturbance may not affect biochemistry of remaining biomass, or 3) bamboo may be resilient to the rates of disturbance in this study. We were, however, unable to test for differences between undisturbed bamboo and either disturbance intensity; future studies would benefit from examination of this potential source of variation in diet selection.

Introduction

The giant panda (*Ailuropoda melanoleuca*) [Chorn and Hoffman, 1978] represents a curious paradox: an herbivorous Carnivore. Descended from carnivorous Ursid ancestors [Gittleman, 1999], the species has transitioned to the lifestyle of a specialist herbivore: 99% or more of the free-ranging diet consists of one item, bamboo [Edwards et al., 2006; Schaller et al., 1985]. In the wild, only a handful of bamboo species among three genera are consumed [Schaller et al., 1985], both leaves and the central, woody stem called culm [Schaller et al., 1985]. Despite numerous adaptations of the skeletal structure for such a diet (e.g., broad, large molars, thickened tooth enamel, enlarged muscular attachments on the skull, and the modified radial sesamoid or "pseudothumb"), the giant panda possesses no adaptations of the digestive tract to assist with fiber digestion [Edwards et al., 2006; Schaller et al., 1985]. Consequently, its digestive efficiency is among the least of all land mammals (10 to 40% on a bamboo-only diet) [Edwards et al., 2006; Long et al., 2004; Schaller et al., 1985; Sims et al., 2007].

Giant pandas show three main adaptations to maximize nutrient availability despite such poor rates of assimilation: 1) energy conservation, 2) maximal intake, and 3) extreme dietary selectivity. Giant pandas conserve scant dietary energy by minimizing all non-feeding activity: in captive pandas, 20 to 30% of daylight hours were spent

feeding, 50 to 55% resting, and 10 to 15% on all other activities [MZS, 2006]. In the wild, in a 24-hour period, 55% of time was spent feeding, 41% resting, and 4% on all other activities [Schaller et al., 1985]. To maximize nutrient intake, giant pandas consume bulk quantities of bamboo, up to 30 kg per day [MZS, 2006; this study, unpublished data]. Even while maintaining these rates of intake, careful dietary selection is exhibited by both wild and captive pandas, in terms of plant part consumed, bamboo species, and individual plants within a species [MZS, 2006; Schaller et al., 1985; Tarou et al., 2005].

However, this selection varies seasonally, again both in the wild and in captivity, particularly with regard to plant-part consumption. During late spring, summer, and autumn, giant pandas consume primarily bamboo leaves; during winter, they shift to a diet composed mainly of culm material. During springtime bamboo-shoot emergence, shoots are consumed preferentially when available, and immediately after this period, animals shift once more to leaf consumption [MZS, 2006; Schaller et al., 1985]. In the wild, these shifts in plant-part selection co-occur with seasonal migrations in altitude, and therefore with changes in bamboo species availability [Reid and Hu, 1991; Schaller et al., 1985]. In captivity, plant-part shifts can occur when consuming the same species of bamboo year-round [MZS, 2006].

The giant panda does face direct threats in the form of poaching or by-catch in snares set for other species [Schaller et al., 1985]. But like many other endangered and threatened species, a greater problem is the pervasive influence of habitat disturbance. The historic range of the species, which once included much of China, has been progressively reduced to smaller areas at higher elevations as bamboo forests have been

turned into agricultural lands. The government of China has made significant strides to control human settlement in wildlife reserves and to reduce the rate of deforestation, however clearing of land for crops or logging of the forest for firewood or raw materials does still occur [WWF, 2004]. Schaller et al. [1985] documented significant and large-scale changes to bamboo life-cycle events as a result of logging. It follows that such disturbances also may impact the biochemical composition of bamboo, and potentially alter its nutritional quality.

Although a great deal of data exist describing what giant pandas consume and when, the specific cues that govern their feeding behavior are still unknown. We postulate that pandas are responding to either 1) seasonal changes in bamboo composition, or 2) circannual rhythms within the pandas themselves, which drive selection for varying suites of nutrients at different times of year. A combination of both factors is even more likely. We sought to investigate the first potential cause for dietary variation, by studying factors that may alter bamboo composition.

Many herbivores have demonstrated an ability to detect compositional differences in feedstuffs and select a diet that matches nutritional requirements while minimizing deleterious compounds. A prevailing hypothesis in nutritional ecology states that digestible energy intake is the principal cue for physiological regulation of feeding rates [Karasov, 1982; Pond et al., 1995; Robbins, 1993]. A number of animal species have demonstrated an ability to control dietary energy, either through compensatory intake or by diet selection, and in some cases selection of concentrated-energy feed items has occurred even in the presence of chemical deterrents [Karasov, 1982; Lewis et al., 2001; Robbins, 1993]. Vertebrates can also control crude protein intake or amino acid profile

by selecting specific feed items or parts of feed [Eshelman and Cameron, 1996; Law, 1992; Lewis et al., 2001; Murphy and Pearcy, 1993; Peitz et al., 1997].

Animals that consume plant matter are often confronted with plant secondary metabolites (allelochemicals), produced by the plant with the specific purpose of deterring herbivory, through digestive inhibition or outright toxicity [Herms and Mattson, 1992; Seigler, 1998]. Such compounds often have a characteristic taste or smell that enables detection and avoidance, and numerous studies have verified a widespread ability among herbivores to select against both types of plant secondary metabolites [Herms and Mattson, 1992; Robbins, 1993]. In addition to chemical defenses, herbivores also select against plant components that impair digestibility or dilute essential nutrients. Plant fiber (structural carbohydrate) is consistently selected against when possible – particularly lignin, its most indigestible form [Pond et al., 1995; Robbins, 1993]. Many plants, particularly those in the grass family, use biogenic silica in addition to fiber to reinforce their structure [Kaufman et al., 1981; Sangster and Parry, 1981]. Silica may decrease digestibility by inhibiting microbial access to cell wall carbohydrates, and may have a negative impact on palatability [Greenway, 1999]. Silicification also may increase as a response to defoliation, indicating a possible secondary role for silica as a defense against herbivory [McNaughton et al., 1985].

Bamboos (Poaceae, Bambusoideae) [Chapman, 1997] represent another paradox, that of a woody grass. As forages, they possess a number of unique characteristics that may drive palatability. Like all grasses, as well as some woody species such as *Populus* spp., bamboos reproduce primarily through vegetative propagation: a parent plant gives rise to underground runners (rhizomes, tillers, or suckers), which grow into genetically

identical daughter stems (ramets) [Landhausser and Lieffers, 1997, 2002; Zasada et al., 1994]. Because this belowground connection is maintained, physiological signaling among ramets is possible, making it possible for the collective to function as one individual (clone) [Li et al., 1998a,b; Wang et al., 2007]. As the tallest of grasses, and one of the few with woody (lignified) central support, bamboos also take on many characteristics of trees, especially with regard to nutrient dynamics [Li et al., 1998a]. However, bamboos are also evergreen: although photosynthetic mechanisms are scaled back in winter, and the oldest leaves may be shed, the plant never loses all of its leaves at once [Li et al., 1998a,b].

Clonal plants demonstrate a strong seasonal cycle of nutrient availability to aboveground and belowground portions of the clone, particularly with regard to non-structural carbohydrates. During the growing season (springtime for temperate species), stored starches from the root system are mobilized to support new growth; during peak photosynthesis (summer), sugars accumulate in the leaves; with the onset of senescence (autumn), soluble sugars from aboveground organs are converted back to stored starches in the central support, roots, and rhizomes [Landhausser and Lieffers, 1997, 2002; Li et al., 1998a; Zasada et al., 1994]. Because aboveground recruitment depends on these belowground reserves, the annual cycle of nutrient flux is very important to maintenance of the stand. Depending on the time of year at which disturbance occurs, removal of aboveground biomass may disrupt the cycle and alter nutrient accumulation in various plant tissues [Li et al., 1998a,b]. Furthermore, because physiological signaling is possible between parts of the clone that are damaged or removed and those that remain,

changes in the biochemical composition of ramets left behind are possible [Wang et al., 2007].

The most immediate and frequently reported effect of plant disturbance that is relevant to herbivores is an increase in plant chemical defenses. Changes in secondary metabolites following disturbance can happen rapidly, as chemical signals are released by damaged tissues [Herms and Mattson, 1992], or they may occur over a longer term, as part of the wound response [Herms and Mattson, 1992; Liese and Weiner, 1997] or as greater allelochemical production in regrowth [Romme et al., 1995]. The only published accounts of antiherbivore defenses in bamboos are among tropical species in Madagascar (e.g., *Cephalostachyum* spp.), some of which contain considerable amounts of cyanogenic glycosides that rapidly convert to hydrogen cyanide when masticated [Glander et al., 1989; Tan, 1999]. There are, however, no published reports in which temperate bamboos have been tested for this compound.

Biogenic silica, on the other hand, is well known in bamboos; bamboos are notorious for large accumulation of silica, even for grasses. Silica deposition varies widely by plant part, with the greatest concentrations detected in the leaves (up to 41% of dry matter in *Sasa* spp.) [Motomura et al., 2002]. Amounts of silica in bamboo leaves have also been shown to increase with season, age, and maturity; the perennial nature of bamboos relative to other grasses may explain their ability to accumulate such large concentrations [Motomura et al. 2002, 2004]. The effect of large or varying concentrations of silica on herbivores such as the giant panda has yet to be examined in detail. However, Schaller et al. [1985] reported a strong negative correlation between

bamboo leaf silicification and leaf consumption by wild pandas, such that during winter, when leaves were rarely consumed, bamboo leaf silica was at its greatest concentrations.

Little to no information exists on the effect of harvest on the biochemistry of bamboos in temperate regions, particularly with regard to giant panda herbivory. However, Reid and Hu [1991] and Wang et al. [2007] observed that wild pandas avoid previously foraged sites. This behavior could simply result from a decrease in available biomass following disturbance [Wang et al., 2007]. On the other hand, it could indicate alterations in any of the variables mentioned previously (fiber characteristics, silicification, carbohydrate or nutrient dynamics) and resulting cues for negative dietary selection. The present study originated in part after anecdotal reports that a pair of captive pandas began to avoid bamboo cut from the same stand(s) after a number of years [J. Tang, Ocean Park Hong Kong, personal communication]. We posited that aboveground disturbance in the form of harvest pressure may alter the biochemistry of the remaining ramets, making them unpalatable to these specialist herbivores.

The present study sought to determine 1) whether disturbance affects palatability of bamboo to herbivorous primary consumers, and 2) what factors drive the seasonal shift in diet selection between leaf and culm portions of the plant.

Methods

To determine whether degree of disturbance affects diet selection by giant pandas, we conducted a series of selection trials over the course of 2.5 years (2006 to 2008). Trials were conducted in conjunction with a larger project studying physiological and compositional changes in bamboo over time and under disturbance. As part of that study, a disturbance treatment in the form of uniform aboveground harvest was applied every 3

months, at a rate of 3% and 20% annual removal of live ramets (Low and High disturbance, respectively). Biomass removed during the application of this treatment was used for all diet selection trials. All bamboo was harvested from 4 subplots within pre-existing bamboo stands at Shelby County AgriCenter (Memphis, TN), operated by Memphis Zoological Society for the purpose of feeding giant pandas at the zoo. The disturbance treatment was first applied in July 2005 (6 months prior to to the start of behavior trials), and continued throughout the remainder of the study.

All trials were conducted at the Memphis Zoo (MZ), with 2 study subjects: a male born in 1998 (international studbook #466), and a female born in 2000 (studbook #507). To provide uniform environmental conditions, selection trials were performed in the indoor exhibit spaces (dayrooms) of the giant panda building (Figure 4.1). To control for the influence of circadian rhythms and daily routine on feeding behavior, all trials were performed during the hour immediately following movement of animals from their off-exhibit sleeping quarters into the dayrooms, which typically occurs between 0700 and 0730 hours. All trials complied with published standards for behavioral research using animal subjects [Animal Behavior, 1992].

As mentioned previously, prior studies with these individual pandas have shown that bamboo-species consumption varies seasonally [MZS, 2006]. However, yellow-grooved bamboo (*Phyllostachys aureosulcata* McClure) is a year-round staple that is reliably consumed regardless of preferences for or against other bamboo species [MZS, 2006]. To remove confounding effects of bamboo species, and to maximize the likelihood of participation by offering a familiar diet item, we chose to use only *P. aureosulcata* for the duration of the study. This is a temperate, rhizomatous bamboo

cultivar that is commonly fed to captive pandas across the United States [Edwards et al., 2006].

During harvest from research subplots, bamboo from the 4 subplots was pooled and bundled according to treatment (Low vs. High disturbance) and transported to MZ within 2 hours of cutting. There, bamboo was sorted into 4 bundles per treatment (8 bundles total per trial), such that all bundles were of similar weight (1.0 to 2.0 kg) and number of ramets per bundle (6 to 13), and of the same approximate leaf-to-culm ratio. Bamboo was then stored in a misted cooler at 16°C until the time of the trial.

Each diet selection trial was conducted during 2 consecutive mornings, in a modified cafeteria-style method. Bamboo from the 2 treatments was distributed in alternating piles in one of 4 pre-determined locations in dayrooms (Figure 4.1). To control for location effects, the position of treatments was switched on Day 2 of each trial – e.g., if on Day 1, piles A and C were Low and piles B and D were High, then on Day 2, piles A and C were High and piles B and D were Low. The treatment assigned to position A on Day 1 was always randomized by coin toss, and placement of piles followed from there. Selection trials occurred on days 2 and 3 after bamboo harvest.

Behavioral observations were conducted via instantaneous-sampling (scan) method. Observations began the moment each panda's nose passed through the door into the room and continued for 30 min, recording the following every 30 seconds: 1) whether the animal was feeding or not, 2) if feeding, from which pile (A through D), and 3) which plant part was being consumed (leaf vs. culm). A second layer of all-occurrence (count) observation was employed to tally the number of times the animal approached each pile, defined as coming within 1/4 body length, or close enough to be aware of the bamboo by

sight and smell. If, at the end of the initial 30-min observation block, the animal was still eating, observations were extended for another 30 min to capture the entirety of the feeding period. Placement of multiple cameras with pivot and zoom capability enabled detailed observation in virtually any location in the room. At least 2 cameras per animal recorded the entire duration of each trial; data were collected through either real-time observation or later video review.

To attempt to identify biochemical cues driving diet preference, we obtained samples of both leaf and culm tissues from each bundle of bamboo before it was placed in dayrooms for behavioral trials. Samples were frozen for analysis and transport to the laboratory, where they were tested for selected compounds that may affect diet selection. The presence or absence of cyanogenic glycosides was tested via multiple survey methods (Feigl-Anger assay, gas chromatography, HPLC; D. Ballhorn, University of Minnesota). Quantification of total starch, as an index of non-structural carbohydrates, was performed using standard methods [AOAC, 2000; M. B. Hall, USDA and University of Wisconsin]. In addition to bamboo sampled during selection trials themselves, routine samples taken from the AgriCenter research plots throughout the year were analyzed for acid-insoluble ash (AIA). In bamboos, AIA represents an accurate and easily-analyzed index for biogenic silica [Greenway, 1999; Tabet et al., 2004].

For statistical analysis, data on each panda were pooled across the 2 trial days (2 hours total of observation). To determine whether selection of Low- vs. High-harvest-rate bamboo changed over time, we employed the Change-Point test, a modification of the Kolmogorov-Smirnov nonparametric one-sample test [Siegel and Castellan, 1988]. To compare leaf consumption and leaf AIA content, as well as culm consumption and

culm starch concentration, we used simple linear correlation [Steel et al., 1997]. AIA data obtained during the month prior to and following each selection trial were pooled, and mean values compared with behavioral data.

We predicted that 1) we would see progressively greater avoidance of highly-disturbed bamboo over time, 2) we would confirm previous reports of seasonal plant-part consumption, 3) we would observe a negative correlation between leaf consumption and leaf silica concentration, and 4) we would observe a positive correlation between culm consumption and culm starch concentration.

Results

During winter 2006 to 2007, Shelby County experienced a stochastic peak in the local population of red-winged blackbirds (*Agelaius phoeniceus*). Due this species' tendency to form large communal flocks in winter, and the attraction of the MZ bamboo stands as a roosting location among agricultural fields, bamboo harvested during January 2007 was covered in excessive bird feces and judged unfit to feed. Therefore, that selection trial could not be performed. Furthermore, the male did not meet our criteria for participation in 3 of the selection trials. To minimize stereotypic behaviors (an animal welfare concern), we set the standard that, if an animal spent more than 15 minutes in any given trial pacing or searching for alternate food items, we would suspend the selection trial and the keepers would offer additional quantities of bamboo from other sites or species. For the April 2008 trial, we could not harvest sufficient biomass to meet minimum quantities of Low-disturbance bamboo for both animals; thus we conducted that trial with the female only.

Diet selection

In total, we collected data from 9 trials involving the female, and 5 trials with the male (Table 4.1). Plant-part selection (Figure 4.2) was consistent between individuals, with the exception of October 2007 through February 2008, when the male shifted from primarily leaf to primarily culm consumption much earlier than the female. Change-point tests detected no significant difference over time in diet selection by harvest intensity (Figure 4.3) for either the female (Z = -1.90; P > 0.05) or the male (Z = -1.06; P > 0.05).

Biochemical analyses

Cyanogenic glycosides were not detected in any of the bamboo samples analyzed. Furthermore, neither concentrations of leaf AIA (r = 0.11; P > 0.10) nor of culm starch (r = -0.42; P > 0.10) correlated significantly with leaf consumption (Figure 4.4; Table 4.1).

Discussion

Seasonal plant-part selection

Giant pandas show distinct preferences for which plant tissues they will consume. Schaller et al. [1985], MZ [2006], and our own studies at Zoo Atlanta (GA) [unpublished data] show that diet selection on the basis of plant part falls into a highly seasonal and predictable pattern. Tarou et al. [2005] and Dierenfeld et al. [1982] observed selection for leaf material from spring through autumn, and Mainka et al. [1989] documented the springtime preference shift from culm to shoots and then leaf. This study confirms earlier observations, with the peak of leaf consumption observed in both July selection trials, and the peak of culm consumption in April of all years. Tabet et al. [2004] found

seasonal differences in bamboo concentrations of protein, fiber fractions, and AIA within a single year. In our own studies, we likewise found seasonal differences in proximate, fiber, and mineral composition; however, seasonal changes were seldom consistent across multiple years [unpublished data]. We undertook the present study under the assumption that cues for seasonal differences in diet selection by giant pandas must be found in finer-scale compositional differences in bamboo.

Given the negative correlation reported by Schaller et al. [1985] between bamboo-leaf silica content and leaf consumption, we expected to observe the same. Although the 1985 report does not infer a cause-and-effect relationship, nor does it indicate whether pandas can detect silica in plant tissues (a requirement for plant defensive compounds), one may infer that greater concentrations of silica could affect nutritional composition through simple dilution, and could likewise affect the taste of forages. However, our study did not show repeatable evidence of such a relationship. During the first year of our study, AIA certainly was present in greater concentrations in winter and spring and lesser concentrations in summer and autumn, but the trend did not hold true for the final year of the study. Tabet et al. [2004] did detect the greatest concentrations of AIA in *P. aureosulcata* in winter, but found intermediate concentrations in spring and summer, and the least AIA in autumn – again, somewhat contrary to the findings of Schaller et al. [1985] in *Sinarundinaria*. McNaughton et al. [1985] postulated that silica could act as a defense against herbivory, but they did not observe actual deterrence of herbivory in grasses with greater silica concentrations; rather, the compound played a role in structural integrity and promotion of compensatory growth following grazing.

Perhaps Schaller et al. [1985] were instead observing an alternate scenario: both silica concentration and bamboo-leaf palatability respond to another set of underlying conditions, e.g., winter and early-spring senescence. Although bamboo leaves do not drop completely during this time of year, photosynthetic capacity is reduced, until after the period of shoot production (for *P. aureosulcata* in this study, starting in May) [Li et al., 1998a]. Reduced protein production and potentially greater proportion of dry matter may result in greater concentrations of inert constituents such as fiber and silica; all of these changes result in less-palatable leaf tissues. In this regard, AIA may still represent a good overall index of bamboo-leaf quality, if not a primary cue for leaf consumption itself. During 2007, the bamboo stand under study experienced a significant flush of new leaf growth and ramet recruitment, likely compensating for damage suffered under drought conditions the year before. New leaves are the most photosynthetically active and least likely to senesce during the pre-shooting period [Li et al., 1998a,b], and this may account for overall low AIA concentrations during the last year of the study.

Perhaps, on the other hand, we were asking the wrong question entirely: rather than wondering why giant pandas avoid leaves in winter, perhaps we should consider why they are attracted to culm. The species' feeding behavior does seem to indicate that during winter and early spring, culm represents a more significant nutritional resource than leaf. What, then, are the animals seeking? In light of the scant data available from this study, we cannot say definitively, however prior qualitative evaluations of bamboo may still point towards non-structural carbohydrates as a significant cue for winter diet selection. Bissell et al. [2006] found colorimetric evidence, via iodine staining, that starch content of culm taken from randomly-sampled *Phyllostachys* spp. is much greater

in March than in September. Because giant pandas are unable to utilize most dietary fiber like other herbivores, digestible or non-structural carbohydrates must represent a significant portion of their energy intake.

In the present study, we sampled culm for starch analysis only during the final 3 selection trials; thus, we lack sufficient data to establish a clear seasonal pattern. However, literature on bamboo and other clonal species support our assumption that stores of non-structural carbohydrates are greater in culm during winter and early spring, and that pandas may be seeking out these stores. Carbohydrate and nutrient dynamics in bamboos seem to follow along the same lines as those of other woody clonal species, with greater non-structural carbohydrate accumulation in leaves in summer, and in culm and rhizomes in late winter [Li et al., 1998a]. Giant panda breeding season typically occurs in mid to late spring, and is characterized by several days or weeks of near-anorexia; perhaps pandas seek out easily-digestible energy sources to build body stores prior to this time.

Indeed, similar curious shifts in plant-part consumption have been anecdotally observed in species with comparable nutritional ecology. The spectacled or Andean bear (*Tremarctos ornatus*) is another herbivorous Ursid, consuming primarily Bromeliaceae and other herbaceous vegetation [Peyton, 1980; Suarez, 1988]. In the past year, however, researchers in Peru have observed spectacled bears consuming roots and trunk portions of trees, and speculate whether they are also exploiting a seasonally-available resource [R. van Horn, San Diego Zoo Global, personal communication]. Again, non-structural carbohydrate storage would be greatest in root and near-ground structures, and spectacled

bears – also lacking anatomical adaptations for fiber digestion [Goldman et al., 2001] – could be seeking out easily-assimilated energy sources.

Finally, clues as to the reasons for giant pandas' seasonal plant-part selection may lie with those individuals that do not conform to the typical pattern. Giant pandas at the San Diego Zoo, unlike elsewhere in the United States, consume a significant amount of culm material year-round [J. Parsons, personal observation]. This location provides pandas with tropical bamboos (e.g., genus *Bambusa*) that would not be possible to cultivate in more temperate locations. Tropical bamboos undergo vegetative propagation in autumn rather than spring, indicating an offset circannual pattern of nutrient flux in these species, compared with temperate bamboos. It is possible that the availability of both tropical and temperate bamboos in San Diego allows those pandas to maximize consumption of limiting nutrients available in culm. Essentially, San Diego pandas may experience a bimodal annual pattern of peak culm consumption, during the pre-recruitment period of each type of bamboo. Again, non-structural carbohydrates represent a likely target for this diet selection and warrant a more careful examination, as almost no prior studies have examined this suite of nutrients in bamboo.

Disturbance effects on diet selection

Aboveground disturbance can have a number of effects on remaining vegetation, which can in turn affect forage palatability. Direct responses of vegetation in the form of plant secondary metabolites have already been mentioned. Positive indirect effects are also possible under moderate disturbance, as gaps in the canopy lead to greater photosynthetic capacity and increased nutrient synthesis [Gurevitch et al., 2002]. Clonal biochemical responses to disturbance are complex, though the one constant in all systems

is a major alteration in nutrient cycling and source-sink dynamics following aboveground perturbations. Removal of clonal shoots from *Populus* spp. dramatically altered carbon metabolism, causing mobilization of free sugars and depletion of starch stores, which in turn stimulated photosynthesis in remaining tissues [Tschaplinski and Blake, 1995]. Harvested tropical bamboo stands in northern India showed greater translocation of nutrients below ground [Tripathi and Singh, 1994]. A number of other studies have reported depletion of stored nutrients in belowground compartments following disturbance events [Landhausser and Lieffers, 1997, 2002; Li et al., 1998a,b; Reichenbacker et al., 1996; Tschaplinski and Blake, 1995; Zasada et al. 1994]. Depletions in culm stores of remaining vegetation could also occur (assuming physiological integration), affecting palatability and nutritional quality of the central stem following severe aboveground alterations. Finally, aboveground disturbance in temperate bamboos can change normal cycles of leaf density, photosynthetic capacity, and recruitment [Li et al. 1998a,b].

For *P. aureosulcata*, we believe that we have ruled out the presence of the most significant allelochemical reported in bamboos. Not only were no cyanogens detected in any samples in this study, independently-submitted fresh samples of *Phyllostachys glauca* and *P. aureosulcata* from our research plots (both shoots and mature tissues) also failed to reveal traces of cyanogenic glycosides [D. Ballhorn, University of Minnesota, personal communication]. We are left to conclude that, at least in these two species and potentially the entire genus, this secondary plant metabolite is not produced. However, a systematic survey of bamboos potentially used as feeds is warranted, particularly in shoot material or new growth, before zoological institutions may feel confident in this

assumption. Because of the presence of cyanogens in at least some genera of tropical bamboos, a greater level of caution should be used when feeding tropical bamboo species.

We did not test for other types of plant defensive compounds in this study, primarily because grasses are not known for allelopathic activity, and we found no further reports in the literature of other compounds that may be present. Liese and Weiner (1997) did detect increased production of unspecified phenolic compounds in response to wounding in several genera of temperate bamboos. Polyphenols comprise a broad class of compounds, including many antioxidants as well as condensed and hydrolysable tannins [Seigler, 1998]; all of these compounds would increase as part of the wound response [Herms and Mattson, 1992; Seigler, 1998]. Again, because grasses are not known to produce tannins, we did not test for these compounds, but for the sake of thoroughness an initial presence-absence survey would be warranted in future studies.

Regardless of the role of plant defensive compounds, we failed to detect a change in diet selection by disturbance treatment over time for either giant panda. It is true that the male's consumption of Low-disturbance bamboo in 2007 to 2008 was greater (> 55%) than in the single 2006 trial in which he participated (< 40%). However, the scant data collected from this individual do not allow for inference. The female's peak consumption of Low-disturbance bamboo (> 55%) came in the last year of the study (July 2007 and February 2008), compared to consumption < 40% during the first two trials. However, again, no clear trend exists to indicate progressive refusal of highly-disturbed bamboo.

Many clonal species are able to mitigate the effects of disturbance or mount a defensive response by taking advantage of physiological integration and sharing of resources among ramets [Herms and Mattson, 1992; Peltzer, 2002; Wilsey, 2002]. Evidence for clonal integration in bamboos is equivocal. Ramets of dwarf bamboo (*Sasa* spp.) do appear to communicate, enabling support of ramets in resource-poor patches by those in resource-rich areas [Saitoh et al., 2002]. Wang et al. [2007], on the other hand, failed to detect any evidence of clonal dynamics in structural response to herbivory. They suggested that ramets were acting as individuals, with hormonally-mediated compartmentalization of stressed portions of the clone [Haukioja, 1991]. The ability of clonal plants to regulate and vary the degree of physiological integration among ramets complicates attempts to characterize disturbance effects.

Although the subplots from which we harvested bamboo were randomized in location, it was possible for Low- and High-disturbance subplots to be physically close together. Dye techniques have been used to identify closely-spaced sister ramets, however a method does not yet exist to identify members of an entire clone [W. Wang and S. B. Franklin, University of Memphis, personal communication] – particularly in rhizomatous as opposed to tillering bamboo species, where sister ramets can be physically distant. Thus, it is very possible that portions of clones in our study straddled subplots. If no physiological integration occurred in these clones, as in Wang et al. [2007], then our subplots were truly independent. However, if this were the case, we would also expect remaining ramets to behave as if no disturbance occurred. If, on the other hand, integration were occurring, disturbance effects may have been mitigated or spread over a larger area, confounding our results. The only true way to parse these two

possibilities would be to plant a bamboo stand such that clones do not overlap, or to identify members of a clone and space treatments out sufficiently that two treatments did not affect a single clone. Because we were working in a relatively small (0.4-ha), already-established stand, neither experimental design was possible.

It is also possible that *P. aureosulcata* is more resilient than we presumed, and 20% annual removal was not a great enough harvest rate to induce biochemical changes in remaining vegetation. We chose disturbance treatments in this study in an attempt to reflect "natural" rates of vegetation removal by grazing wild pandas (3% annual removal) [Wang et al., 2007] versus removal rates typically practiced by zoos when feeding exotic species (20%; based on our previous observations at Memphis Zoo). Perhaps a greater amount of disturbance would be necessary before significant changes in clonal dynamics occurred. Likewise, the timing and degree of disturbance matters a great deal in clonal species. If ramets are removed during the belowground storage period, nutrient loss to the clone is not significant, and growth and composition of resulting new ramets is not affected. If, on the other hand, aboveground biomass is removed during peak photosynthesis, the ability of the clone to muster sufficient nutrients to support normal physiological function is compromised [Li et al., 1998a,b, Shanmughavel and Francis, 1996, 2001; Tripathi and Singh, 1994]. Our harvest treatments were spread out across an entire year; if treatment application had been concentrated during a particular period of time, other effects may have been observed.

Given the lack cyanogenic activity in *P. aureosulcata*, it is entirely possible that ramets in this study failed to respond to disturbance in a way that was meaningful to herbivores. This does not mean, however, that intense disturbance does not impact the

bamboo stand as a whole, with indirect effects on forage palatability. We have shown elsewhere that bamboo disturbance has significant effects on life-stage processes such as recruitment and mortality [unpublished data]. Our subplots happened to be located in a young, establishing stand, with a high rate of recruitment and a large percentage of new growth among the material offered during behavior trials. In a more mature stand with lower rates of recruitment, the same harvest rates could leave behind progressively older, more lignified growth [Liese and Weiner, 1997] – particularly if harvesting occurred primarily at the edge of a stand or row, as is convenient. This study did not investigate the effects of such skewed harvesting, choosing instead to harvest in a uniform manner throughout the stand, in an attempt to duplicate herbivore foraging patterns and a more sustainable method of bamboo management. For the health of the stand and to maximize palatability, bamboo should be managed such that the oldest growth is continually harvested, allowing the newest growth to mature and support the clone. This management regime parallels the normal growth pattern of healthy bamboo stands, with the oldest ramets becoming overshaded and senescing [Shanmughavel and Francis, 2001; Tripathi and Singh, 1994]. Mimicking the normal bamboo life cycle ensures minimal impact on natural dynamics of nutrient flux.

Finally, although animals in this study did not perceive qualitative differences in forage quality between highly-disturbed and less-disturbed bamboo, nutritional quality alone is not a sole consideration when feeding animals in captivity, or when managing landscapes for free-ranging populations. Although a moderate level of disturbance may have beneficial effects [Gurevitch et al., 2002], negative effects of too much disturbance are possible if the clone's ability to gather resources is limited [Li et al., 1998a,b], or if

the rate of harvest itself is greater than rates of recruitment. In light of the aforementioned dry-matter intake rates of which giant pandas are capable, sustainable bamboo-stand management is fundamental to ensuring long-term forage availability.

We must, in the final analysis, recognize 2 key limitations of this study. First, we were limited in our use of bamboo material for diet-selection trials to only 2 of the bamboo-disturbance treatments applied during the course of our larger study. A third treatment, Control (no bamboo removal) also existed within the AgriCenter bamboo study site. However, for obvious reasons, Control bamboo could not be removed for diet-selection testing without compromising the study design. It is entirely possible that giant pandas might have consumed Control bamboo at a different rate than either Low- or High-disturbance bamboo, and we merely detected no difference in consumption of bamboo already affected by disturbance.

Second, this is an examination of the behavior of only 2 zoo-housed animals in a single location. Without replication, we cannot extend inference to other captive pandas, and we further recognize that conditions in zoos do not represent those experienced by wild populations. To our knowledge, only 1 other investigation of a preliminary nature [Tabet et al., 2004] attempted to answer the seasonal diet-selection riddle from the perspective of bamboo biochemical composition or physiology. Replication of our study conditions at other zoological institutions worldwide would be extremely useful in answering important questions regarding captive management of pandas and their food supply.

At the same time, a closer examination of free-ranging giant panda diet selection, particularly in habitats experiencing anthropogenic manipulation, could help to guide

land-management decisions affecting wild populations. Schaller et al. [1985] and Wang et al. [2006] did not examine diet selection directly, but did answer several preliminary questions regarding habitat and herbivore responses to disturbance. Hunter et al. [2003] looked at the concept of habitat restoration from a nutrient-availability perspective; such a study could be expanded to examine the effects of habitat restoration on giant panda diet selection as well. All are important questions for species-level conservation efforts, and merit investigation in multiple locations within the giant panda's native range. The keys to conservation of the giant panda are habitat restoration and finding a way to allow for human presence while maintaining suitable animal habitat [WWF, 2004]. An understanding of the nutritional ecology of this species and the nature of panda-bamboo interactions is essential to navigating this balance, and to the success of future conservation endeavors.

Conclusions

1. Previously-reported seasonal patterns of leaf versus culm consumption were confirmed: giant pandas consumed more *Phyllostachys aureosulcata* leaves in summer and autumn, and more culm in winter and early spring.
2. For *P. aureosulcata*, no significant correlations were detected between plant-part consumption and either silica (AIA) content in leaves or starch content in culms.
3. No significant changes in diet selection over time were detected between more- or less-disturbed *P. aureosulcata* (3% versus 20% annual removal rates).
4. Cyanogenic glycosides were not detected in any samples of *P. aureosulcata.*

Table 4.1 Summary of diet selection trials at the Memphis Zoo.

Date[1]	Animal ID[2]	Length of trial[3] (min)	Time spent eating (%)	Time at treatment (% of time eating)[4]		Plant-part consumption (% of time eating)[5]		Dry-matter concentration (%) in plant tissues	
				3%	20%	Leaf	Culm[6]	AIA in leaves[7]	Starch in culm[8]
11-Jan-06	M466	–	–	–	–	–	–	–	–
	F507	90	90.00	28.40	71.60	43.83	42.59		
9-Apr-06	M466	60	67.50	38.27	61.73	2.47	67.90	6.33 (0.67)	–
	F507	120	91.25	35.16	64.84	0.46	79.45		
10-Jul-06	M466	–	–	–	–	–	–	4.59 (0.74)	–
	F507	120	80.42	53.89	46.11	58.55	9.84		
23-Oct-06	M466	–	–	–	–	–	–	4.67 (0.27)	–
	F507	90	89.44	48.45	51.55	45.34	31.06		
2-Apr-07	M466	120	65.00	66.03	33.97	7.05	83.33	5.15 (0.34)	–
	F507	120	85.00	47.06	52.94	8.82	81.37		
19-Jul-07	M466	120	88.75	62.91	37.09	79.34	11.74	–	–
	F507	120	85.83	70.39	29.61	77.67	10.68		
29-Oct-07	M466	120	83.33	58.08	41.92	5.00	90.00	–	6.88 (1.30)
	F507	120	61.25	50.52	49.49	65.99	23.13		
4-Feb-08	M466	120	90.00	56.78	43.22	2.78	87.96	–	5.18 (1.10)
	F507	120	72.50	59.86	40.15	47.13	41.95		
7-Apr-08	M466	–	–	–	–	–	–	1.68 (0.19)	8.54 (0.40)
	F507	120	94.63	40.58	59.42	0.00	84.72		

[1]Refers to the first day of a two-day trial

[2]M466 refers to the male panda; F507 refers to the female

[3]Comprises two half-trials performed at the same time of day on successive days; pandas are observed for 30-minute blocks of time from the point at which they are let into the room with pre-placed piles of bamboo until they are finished eating

[4]Disturbance treatment (uniform harvest) administered quarterly, at a rate of 3% or 20% annual removal of individual ramets.

[5]Handling time and incidental consumption of other plant parts (e.g., branches) were counted as a portion of time spent eating, but not included in leaf or culm consumption

[6]Culm = central, woody stem

[7]Acid-insoluble ash, mean (SE) of samples from subplots in which selection-trial bamboo was grown, taken within 1 month of trial date.

[8]Mean (SE) of tissues sampled from bamboo used for selection trials

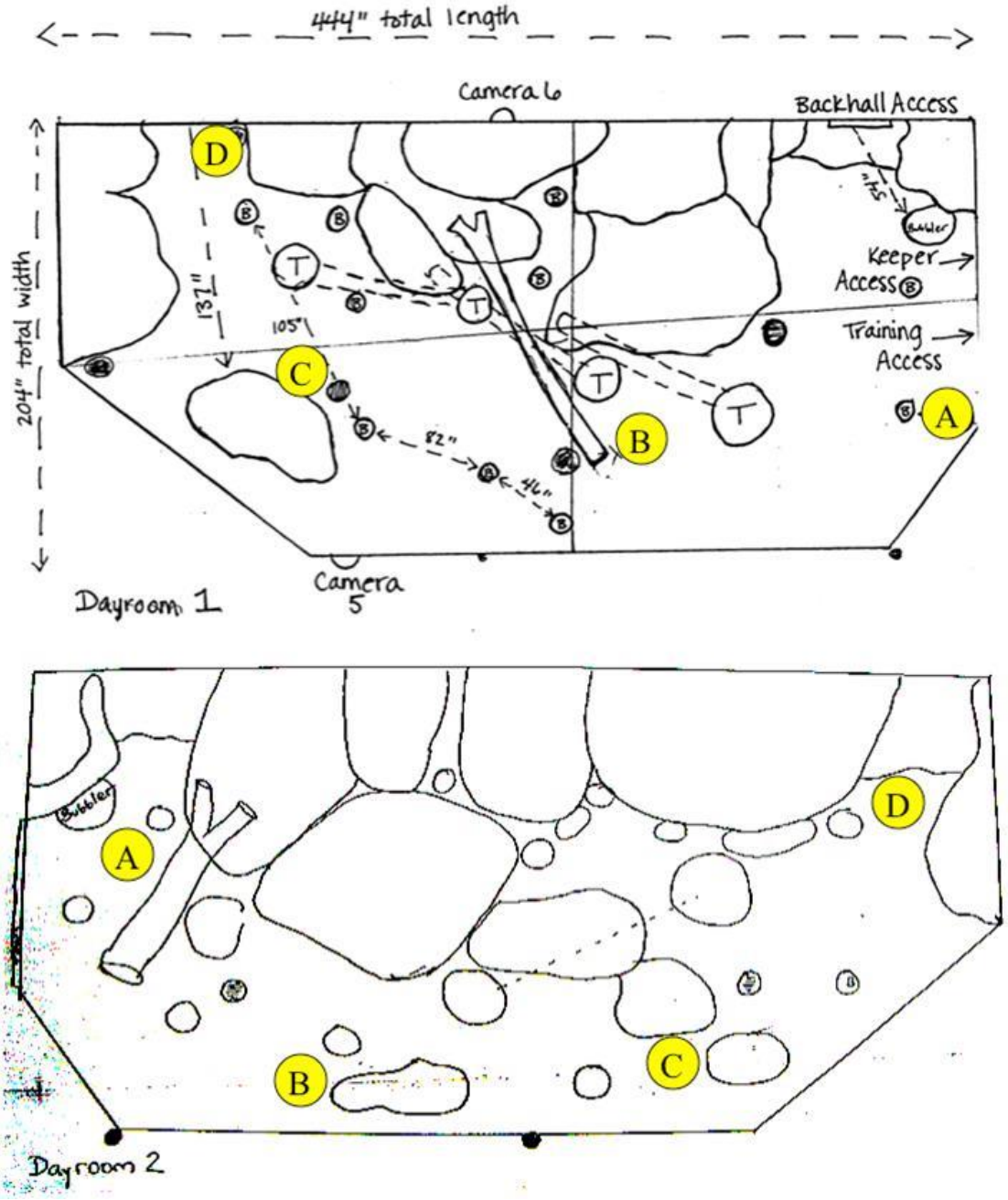

Figure 4.1 Indoor giant panda enclosures at the Memphis Zoo.

Diet selection trials were conducted entirely within these 2 enclosures: Dayroom 1 was used by the female (international studbook #507), and Dayroom 2 was used by the male (studbook #466). Letters indicate placement of *Phyllostachys aureosulcata* bamboo from two treatments, High disturbance (20% annual biomass removal) and Low disturbance (3% annual removal), such that treatments were placed in 4 alternating piles.

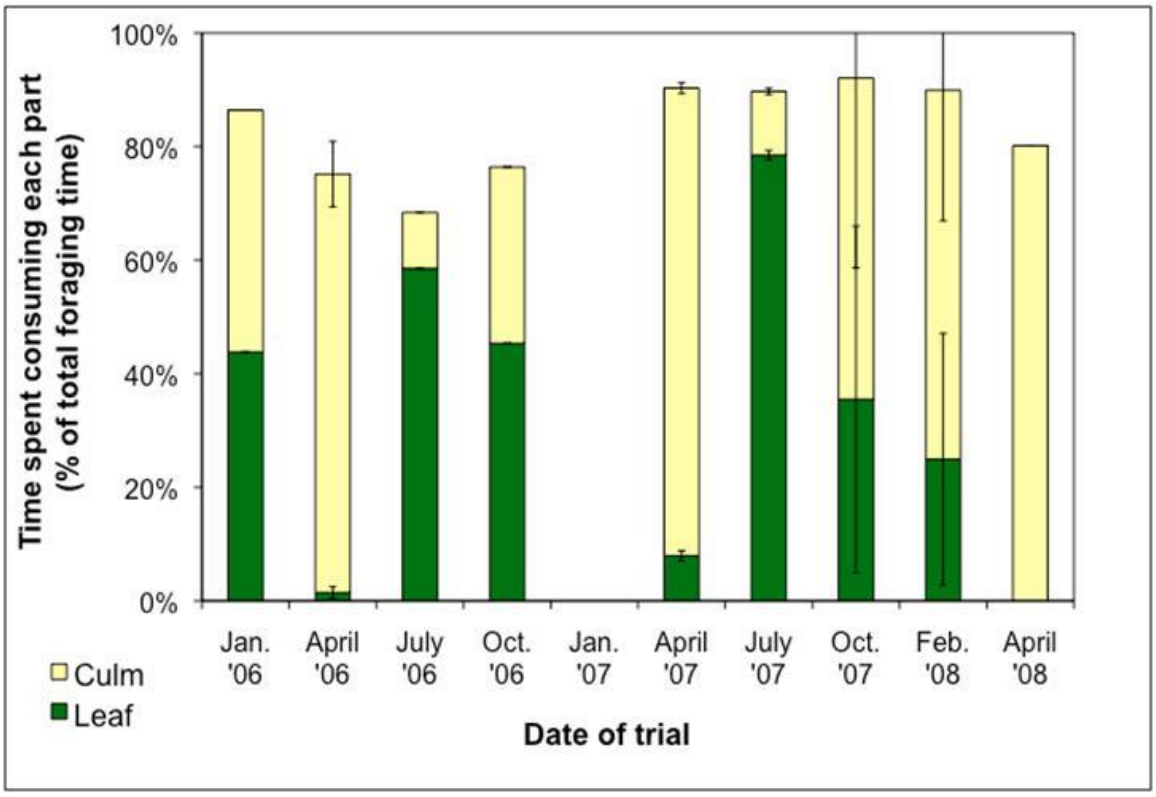

Figure 4.2 Plant-part selection of *Phyllostachys aureosulcata* bamboo by giant pandas.

Diet selection trials were conducted at the Memphis Zoo, with an adult male (international studbook #466) and an adult female (studbook #507). Green bars indicate proportionate consumption of bamboo leaves (% of total foraging time); tan bars indicate consumption of culm (central woody stalk). Standard error of mean observations are indicated when both pandas participated in a given trial. The male did not meet criteria for data collection in January, July, and October 2006, or April 2008. In January 2007, bamboo harvested from study plots was not of sufficient quality to feed.

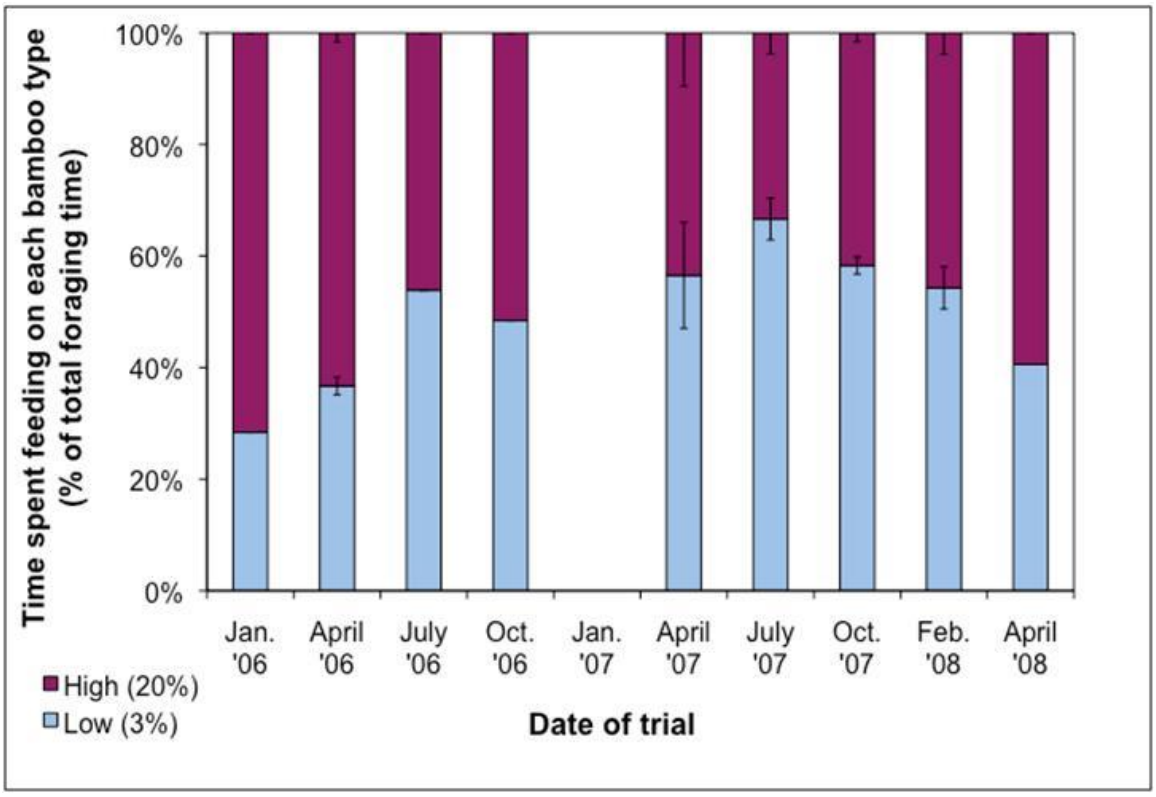

Figure 4.3 Diet selection of giant pandas by bamboo disturbance treatment.

Diet selection trials were conducted at the Memphis Zoo, with an adult male (international studbook #466) and an adult female (studbook #507). Blue bars indicate proportionate consumption (% of total foraging time) of *Phyllostachys aureosulcata* bamboo from Low-disturbance subplots (3% annual removal of aboveground biomass); maroon bars indicate consumption of bamboo from High-disturbance subplots (20% annual removal). Standard error of mean observations are indicated when both pandas participated in a given trial. The male did not meet criteria for data collection in January, July, and October 2006, or April 2008. In January 2007, bamboo harvested from study plots was not of sufficient quality to feed.

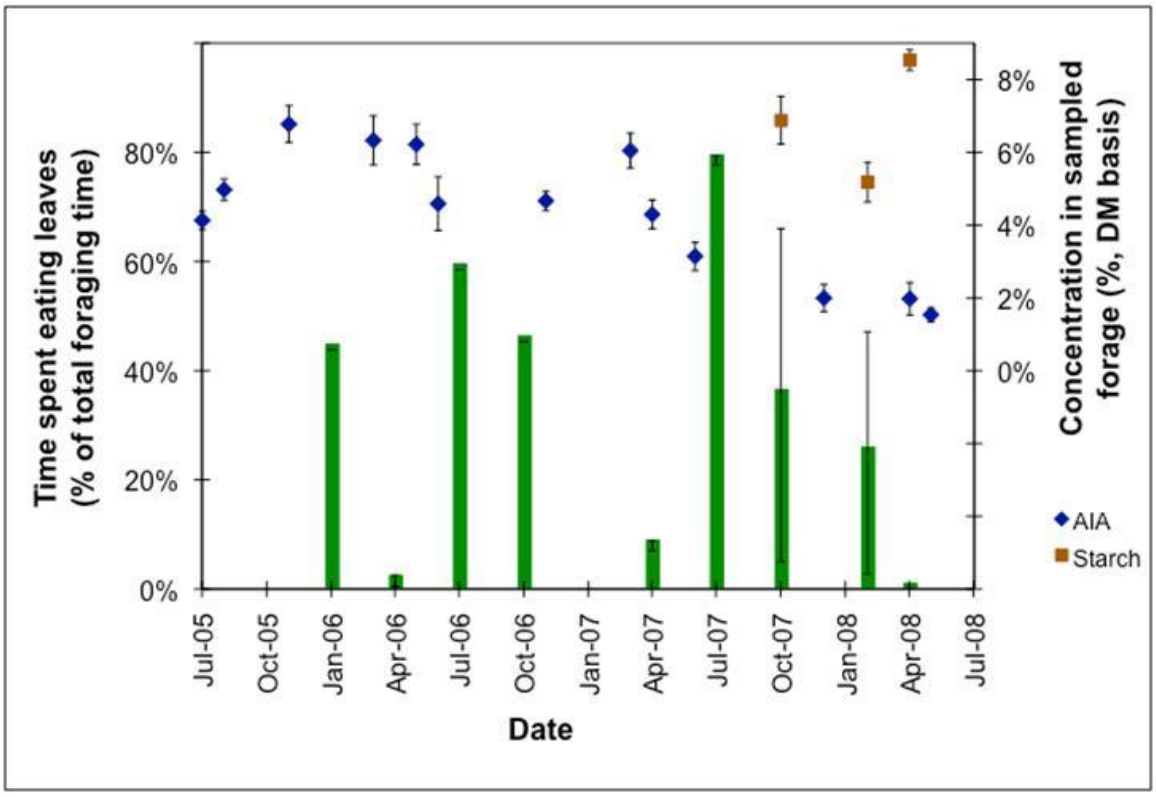

Figure 4.4 Bamboo leaf selection by giant pandas, compared with silica and starch concentration of bamboo tissues.

Phyllostachys aureosulcata leaf selection (% of total foraging time) is represented on the left-side axis; leaf acid-insoluble ash (AIA) and culm (central stem) starch are represented on the right-side axis. Diet selection trials were conducted at the Memphis Zoo, with an adult male (international studbook #466) and an adult female (studbook #507). AIA, an index of biogenic silica, was analyzed in bamboo-stand samples during the month prior to and following each selection trial. Starch was analyzed in bamboo samples taken during selection trials. Bars indicate standard error of the mean

REFERENCES

Animal Behaviour. (1992) Guidelines for the use of animals in research. Animal Behavior 43:185-188.

Alpert P. and Mooney H.A. (1986) Resource sharing among ramets in the clonal herb, *Fragaria chiloensis*. Oecologia 70:227-233.

AOAC. (2000) Official methods of analysis, 17th edn. Arlington, VA: Association of Official Analytical Chemists.

Belsky A.J., Carson W.P., Jensen C.L. and Fox G.A. (1993) Overcompensation by plants: herbivore optimization or red herring? Evolutionary Ecology 7:109-121.

Bissell H.A., Wang H.L. and Rude B.J. (2006) Seasonal histochemical, morphological, and nutritional characteristics of bamboo selected by giant pandas. In: Proceedings of the Ecological Society of America, Memphis, TN.

Bleijenberg M.C.K. and Nijboer J. (1989) Feeding herbivorous carnivores. In: Glatston AR. (ed) Red panda biology, pp. 41-50. The Hague, Netherlands: SPB Academic Publishing.

Breuning-Madsen H., Ehlers-Koch C., Gregersen J. and Lund Løjtnant C. (2010) Influence of perennial colonies of piscivorous birds on soil nutrient contents in a temperate humid climate. Geografisk Tidsskrift-Danish Journal of Geography, 110, 25–35.

Chapman G.P. (1997) The bamboos: a background to current research. In: Chapman G.P. (ed) The bamboos, pp. 3-13. San Diego, CA: Academic Press.

Chorn J. and Hoffmann R.S. (1978) *Ailuropoda melanoleuca*. Mammalian Species, 110, 1-6.

Clark L. (2006) Bamboo biodiversity. www.eeob.iastate.edu/research/bamboo/bamboo.html. Accessed 23 January 2013.

de Kroon H. (2005) Competition between shoots in stands of clonal plants. Plant Species Biology 8:85-94.

de Kroon H. and Kalliola R. (1995) Shoot dynamics of the giant grass *Gynerium sagittatum* in Peruvian floodplains, a clonal plant that does show self-thinning. Oecologia 101:124-131.

Dierenfeld, E.S. (1997) Chemical composition of bamboo in relation to giant panda nutrition. Pp. 205-211 in The bamboos (G. P. Chapman, ed.). Academic Press, San Diego, California.

Dierenfeld E.S., Hintz H.F., Robertson J.B., Van Soest P.J. and Oftedal O.T. (1982) Utilization of bamboo by the giant panda. Journal of Nutrition 112:636–41.

Edwards M.S., Zhang G., Wei R. and Liu X. (2006) Nutrition and dietary husbandry. In: Wildt D.E., Zhang A., Zhang H., Janssen D.L., and Ellis S. (eds) Giant pandas: Biology, veterinary medicine and management, pp. 101-158. New York, NY: Cambridge University Press.

Eshelman B.D. and Cameron G.N. (1996) Experimentally induced habitat shifts by hispid cotton rats (*Sigmodon hispidus*): response to protein supplementation. Journal of Mammalogy 77:232-239.

Fang, J.-Y., Wang G. G., Liu G.-H. and Xu S.-L. (1998) Forest biomass of China: an estimate based on the biomass-volume relationship. Ecological Applications 8:1084-1091.

Garcia L.V., Marañon T., Ojeda F., Clemente L., and Redondo R. (2002) Seagull influence on soil properties, chenopod shrub distribution, and leaf nutrient status in semi-arid Mediterranean islands. Oikos, 98, 75-86.

Gittleman JL. (1999) Hanging bears from phylogenetic trees: investigating patterns of macroevolution. Ursus 11:29-39.

Glander KE, Wright PC, Seigler DS, Randrianasolo V, Randrianasolo B. (1989) Consumption of cyanogenic bamboo by a newly discovered species of bamboo lemur. American Journal of Primatology 19:119-124.

Goldman I, Silver SC, Dierenfeld ES. (2001) Passage and digestion in the spectacled bear (*Tremarctos ornatus*) fed a zoo-based diet moderately high in fiber. In: Proceedings of the American Zoo and Aquarium Association Nutrition Advisory Group Fourth Conference on Zoo and Wildlife Nutrition, Lake Buena Vista, FL.

Gough L., Goldberg D.E., Hershock C., Pauliukonis N. and Petru M. (2002) Investigating the community consequences of competition among clonal plants. Evolutionary Ecology, 15, 547-563.

Greenway S.L. (1999) Evaluation of bamboo as livestock forage and applications of *Yucca schidigera* and *Quillaja saponaria* products in agriculture, M.S. thesis, United States: Oregon State University.

Gurevitch J, Scheiner SM, Fox GA. (2002) The ecology of plants. Sunderland, MA: Sinauer Associates. 523 p.

Haukioja E. (1991) The influence of grazing on the evolution, morphology and physiology of plants as modular organisms. Philosophical Transactions of the Royal Society B, 333, 241-247.

Herms D.A. and Mattson W.J. (1992) The dilemma of plants: to grow or defend. Quarterly Review of Biology, 67, 283-335.

Hirayama K., Kawamura S., Mitsuoka T. and Tashiro K. (1989) The faecal flora of the giant panda (*Ailuropoda melanoleuca*). Journal of Applied Bacteriology 67:411-415.

Hopkins W.G. and Huner N.P.A. (2004) Introduction to plant physiology, 3rd edn. London, Ontario: John Wiley and Sons.

Hunter I.R., Dierenfeld E.S. and Jinhe F. (2003) The possible nutritional consequences for giant panda of establishing reserve corridors with various bamboo species. Journal of Bamboo and Rattan, 2, 167-178.

Karasov W.H. (1982) Energy assimilation, nitrogen requirement, and diet in free-living antelope ground squirrels, *Ammospermophilus leucurus*. Physiological Zoology 55:378-392.

Kaufman P.B., Dayanandan P., Takeoka Y., Bigelow W.C., Jones J.D., Iler R. 1981. Silica in shoots of higher plants. In: Simpson T.L., Volcani B.E., editors. Silicon and siliceous structures in biological systems. New York: Springer-Verlag. p 409-449.

Keeley J.E. and Bond W.J. (1999) Mast flowering and semelparity in bamboos: the bamboo fire cycle hypothesis. The American Naturalist, 154, 383-391.

Kleinhenz V. and Midmore D.J. (2001) Aspects of bamboo agronomy. In: Sparks D.L. (ed) Advances in Agronomy, Vol. 74, pp. 99-145. London, UK: Academic Press.

Klimes L. and Klimesova J. (2002) The effects of mowing and fertilization on carbohydrate reserves and regrowth of grasses: do they promote plant coexistence in species-rich meadows? Evolutionary Ecology, 15, 363-382.

Kramberger B. and Klemencic S. (2003) Effect of harvest date on the chemical composition and nutritive value of *Cerastium holosteoides*. Grass and Forage Science, 58, 12-16.

Landhausser S.M. and Lieffers V.J. (1997) Seasonal changes in carbohydrate storage and regrowth in rhizomes and stems of four boreal forest shrubs: applications in *Picea glauca* understorey regeneration. Scandinavian Journal of Forest Research, 12, 27-32.

Landhausser S.M. and Lieffers V.J. (2002) Leaf area renewal, root retention and carbohydrate reserves in a clonal tree species following above-ground disturbance. Journal of Ecology, 90, 658-665.

Law BS. (1992) The maintenance requirements of the Queensland blossom bat (*Syconycteris australis*) on a sugar/pollen diet: is nitrogen a limiting resource? Physiological Zoology 65:634-648.

Lewis CE, Clark TW, Derting TL. (2001) Food selection by the white-footed mouse (*Peromyscus leucopus*) on the basis of energy and protein contents. Canadian Journal of Zoology 79:562-568.

Li R., Werger M.J.A., During H.J. and Zhong Z.C. (1998a) Carbon and nutrient dynamics in relation to growth rhythm in the giant bamboo *Phyllostachys pubescens*. Plant and Soil, 201,113-123.

Li R., Werger M.J.A., During H.J. and Zhong Z.C. (1998b) Biennial variation in production of new shoots in groves of the giant bamboo *Phyllostachys pubescens* in Sichuan, China. Plant Ecology, 135, 103-112.

Li X. (2004) Physical, chemical, and mechanical properties of bamboo and its utilization potential for fiberboard manufacturing, M.S. thesis, United States: Louisiana State University.

Liese W. and Weiner G. (1997) Modifications of bamboo culm structures due to ageing and wounding. In: Chapman G.P. (ed) The bamboos, pp. 314-322. San Diego, CA: Academic Press.

Long Y., Lu Z., Wang D., Zhu X., Wang H., Zhang Y. and Pan W. (2004) Nutritional strategy of giant pandas in the Qinling Mountains of China. In: Lindburg D. and Baragona K. (eds) Giant pandas: Biology and conservation, pp. 90-100. Berkeley, CA: University of California Press.

Mainka SA, Zhao G, Li M. (1989) Utilization of a bamboo, sugar cane, and gruel diet by two juvenile giant pandas (*Ailuropoda melanoleuca*). Journal of Zoo and Wildlife Medicine 20:39–44.

McClure F.A. (1966) The bamboos. Cambridge, MA: Harvard University Press.

McNaughton S.J. (1983) Compensatory plant growth as a response to herbivory. Oikos 40:329-336.

McNaughton S.J. (1984) Grazing lawns: animals in herds, plant form, and coevolution. American Naturalist 124:863-886.

McNaughton SJ, Tarrants JL, McNaughton MM, Davis RH. (1985) Silica as a defense against herbivory and a growth promotor in African grasses. Ecology 66:528-535.

Motomura H, Mita N, Suzuki M. (2002) Silica accumulation in long-lived leaves of *Sasa veitchii* (Carriere) Rehder (Poaceae – Bambusoideae). Annals of Botany 90:149-152.

Motomura H, Fujii T, Suzuki M. 2004. Silica deposition in relation to ageing of leaf tissues in *Sasa veitchii* (Carriere) Rehder (Poaceae – Bambusoideae). Annals of Botany 93:235-248.

Murphy R.J. and Alvin K.L. (1997) Fibre maturation in bamboos. In: Chapman G.P. (ed) The bamboos, pp. 293-303. San Diego, CA: Academic Press.

Murphy ME, Pearcy SD. (1993) Dietary amino acid complementation as a foraging strategy for wild birds. Physiology and Behavior 53:689-698.

MZS. (2004) Annual report to the U.S. Fish and Wildlife Service: summary of research activities under PRT-052166. Memphis Zoological Society.

MZS. (2005) Annual report to the U.S. Fish and Wildlife Service: summary of research activities under PRT-052166. Memphis Zoological Society.

MZS. (2006) Annual report to the U.S. Fish and Wildlife Service: summary of research activities under PRT-052166. Memphis Zoological Society.

Nickley J.K. (2001) Giant pandas: bamboo intake and fecal analysis, M.S. thesis, United States: California State Polytechnic University – Pomona.

Olmos F, Galetti M, Paschoal M, Mendes SL. (1993) Habits of the Southern bamboo rat, *Kannabateomys amblyonyx* (Rodentia, Echimyidae) in Southeastern Brazil. Mammalia 57:325-336.

Peitz DG, Lochmiller RL, Leslie DM Jr, Engle DM. (1997) Protein quality of cottontail rabbit forages following rangeland disturbance. Journal of Range Management 50:450-458.

Peltzer D.A. (2002) Does clonal integration improve competitive ability? A test using aspen (*Populus tremuloides* [Salicaceae]) invasion into prairie. American Journal of Botany, 89, 494-499.

Peyton, B. (1980) Ecology, distribution, and food habits of spectacled bears, *Tremarctos ornatus*, in Peru. Journal of Mammalogy 61:639-652.

Piqueras J., Klimes L. and Redbo-Torstensson P. (1999) Modelling the morphological response to nutrient availability in the clonal plant *Trientalis europaea* L. Plant Ecology 141:117-127.

Pond WG, Church DC, Pond KR, Schoknecht PA. (2005) Basic animal nutrition and feeding. 5th Edition. New York: John Wiley and Sons. 580 p.

Price E.A.C. and Marshall C. (1999) Clonal plants and environmental heterogeneity: an introduction to the proceedings. Plant Ecology, 141, 3-7.

Recht C. and Wetterwald M.F. (1996) Bamboos. Portland, OR: Timber Press.

Reed B. (2009) National Zoo desperately seeks bamboo. http://www.npr.org/templates/story/story.php?storyId=99677708. Released 21 January 2009; accessed 21 February 2013. National Public Radio.

Reichenbacker R.R., Schultz R.C. and Hart E.R. (1996) Artificial defoliation effect on *Populus* growth, biomass production, and total nonstructural carbohydrate concentration. Environmental Entomology, 25, 632-642.

Reid D.G. and Hu J. (1991) Giant panda selection between *Bashania fangiana* bamboo habitats in Wolong Reserve, Sichuan, China. Journal of Applied Ecology, 28, 228-243.

Renvoize S.A. and Hodkinson T.R. (1997) Classification of *Phyllostachys*. In: Chapman G.P. (ed) The bamboos, pp. 95-106. San Diego, CA: Academic Press.

Robbins C.T. (1993) Wildlife feeding and nutrition, 2nd edn. San Diego, CA: Academic Press.

Romme WH, Turner MG, Wallace LL, Walker JS. (1995) Aspen, elk and fire in northern Yellowstone National Park. Ecology 76:2097-2106.

Rothman J.M., Plumptre A.J., Dierenfeld E.S. and Pell A.N. (2007) Nutritional composition of the diet of the gorilla (*Gorilla beringei*): a comparison between two montane habitats. Journal of Tropical Ecology, 23, 673-682.

Saitoh T., Seiwa K. and Nishiwaki A. (2002) Importance of physiological integration of dwarf bamboo to persistence in forest understorey: a field experiment. Journal of Ecology, 90, 78-85.

Sangster AG, Parry SW. (1981) Ultrastructure of silica deposits in higher plants. In: Simpson TL, Volcani BE, editors. Silicon and siliceous structures in biological systems. New York: Springer-Verlag. p 383-407.

SAS Institute, Inc. (2012) SAS/STAT user's guide. Release 9.3. Cary, NC: SAS Institute Inc.

Schaller G.B., Hu J., Pan W. and Zhu J. (1985) The giant pandas of Wolong. Chicago, IL: University of Chicago Press.

Seigler DS. (1998) Plant secondary metabolism. Boston, MA: Kluwer Academic Publishers.

Shanmughavel P. and Francis K. (1996) Biomass and nutrient cycling in bamboo (*Bambusa bambos*) plantations of tropical areas. Biology and Fertility of Soils, 23, 431-434.

Shanmughavel P. and Francis K. (2001) Bioproductivity and nutrient cycling in bamboo and acacia plantation forests. Bioresource Technology, 80, 45-48.

Siegel S, Castellan NJ. (1988) Nonparametric statistics for the behavioral sciences. 2nd Edition. New York: McGraw-Hill. 399 p.

Sims J.A., Parsons J.L., Bissell H.A., Sikes R.S., Ouellette J.R. and Rude B.J. (2007) Determination of bamboo-diet digestibility and fecal output by giant pandas. Ursus, 18, 38-45.

Steel RGD, Torrie JH, Dickey DA. (1997) Principles and procedures of statistics: a biometrical approach. 3rd Edition. New York: McGraw-Hill. 666 p.

Stern M.J., Goodell K. and Kennard D.K. (1999) Local distribution of *Chusquea tomentosa* (Poaceae: Bambusoideae) before and after a flowering event. Biotropica 31:365-368.

Stuefer J.F., Erschbamer B., Huber H. and Suzuki J-I. (2002) The ecology and evolutionary biology of clonal plants: an introduction to the proceedings of *Clone-2000*. Evolutionary Ecology 15:223-230.

Stuefer J.F., Gomez S. and Van Molken T. (2004) Clonal integration beyond resource sharing: implications for defence signaling and disease transmission in clonal plant networks. Evolutionary Ecology 18:647-667.

Suarez, L. (1988) Seasonal distribution and food habits of spectacled Bears Tremarctos *ornatus* in the highlands of Ecuador. Studies on Neotropical Fauna and Environment 23:133-136.

Tabet R.B., Oftedal O.T. and Allen M.E. (2004) Seasonal differences in composition of bamboo fed to giant pandas (*Ailuropoda melanoleuca*) at the National Zoo. In: Baer C.K. (ed) Symposia of the Comparative Nutrition Society 2004: Proceedings of the 5th Comparative Nutrition Society Symposium, Hickory Corners, MI, pp. 176-180.

Tan C.L. (1999) Group composition, home range size, and diet of three sympatric bamboo lemur species (genus *Hapalemur*) in Ranomafana National Park, Madagascar. International Journal of Primatology, 20, 547-566.

Tarou L.R., Williams J., Powell D.M., Tabet R. and Allen M. (2005) Behavioral preferences for bamboo in a pair of captive giant pandas (*Ailuropoda melanoleuca*). Zoo Biology, 24, 177-183.

Taylor A.H. and Qin Z. (1993) Structure and dynamics of bamboos in the Wolong Natural Reserve, China. American Journal of Botany 80:375-384.

Tolvanen A., Schroderus J. and Henry G.H.R. (2002) Age- and stage-based bud demography of *Salix arctica* under contrasting muskox grazing pressure in the High Arctic. Evolutionary Ecology 15: 443–462.

Tripathi S.K. and Singh K.P. (1994) Productivity and nutrient cycling in recently harvested and mature bamboo savannas in the dry tropics. Journal of Applied Ecology, 31, 109-124.

Tschaplinski T.J. and Blake T.J. (1995) Growth and carbohydrate status of coppice shoots of hybrid poplar following shoot pruning. Tree Physiology, 15, 333-338.

USDA. 2012. Plant guide: giant cane, *Arundinaria gigantea* Mulhl. Accessed from http://plants.usda.gov/java/profile?symbol=ARGI, 26 April 2013. United States Department of Agriculture Natural Resources Conservation Service.

Van Soest P.J., Robertson J.B. and Lewis B.A. (1991) Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. Journal of Dairy Science, 74, 3583–3597.

Vazquez-Lopez J.M., Vibrans H., Garcia-Moya E., Valdez-Hernandez J.I., Romero-Manzanares A. and Cuevas-Guzman R. (2004) Effects of harvesting on the structure of a neotropical woody bamboo (*Otatea*: Guaduinae) populations. Interciencia 29:207-211.

Wang, T. (2003) Habitat analysis for giant panda in Laoxiancheng nature reserve in the Qinling Mountaings, China. M.S. thesis, Enschede, The Netherlands: International Institute for Geo-Information Science and Earth Observation.

Wang W., Franklin S.B., Ren Y. and Ouellette J.R. (2006) Growth of bamboo *Fargesia qinlingensis* and regeneration of trees in a mixed hardwood-conifer forest in the Qinling Mountains, China. Forest Ecology and Management 234:107-115.

Wang W., Franklin S.B. and Ouellette J.O. (2007) Clonal regeneration of an arrow bamboo, *Fargesia qinlingensis*, following giant panda herbivory. Plant Ecology, 192, 97-106.

Wilsey B. (2002) Clonal plants in a spatially heterogeneous environment: effects of integration on Serengeti grassland response to defoliation and urine-hits from grazing mammals. Plant Ecology, 159, 15-22.

WWF. (2004) New survey reveals nearly 1,600 giant panda in the wild. Press Release, www.wwfchina.org. 10 June 2004. World Wildlife Fund-China

Young K.R. (1991) Natural history of an understory bamboo (*Chusquea* sp.) in a tropical timberline forest. Biotropica 23:542-554.

Zasada J.C., Tappeiner III J.C., Maxwell B.D. and Radwan M.A. (1994) Seasonal changes in shoot and root production and in carbohydrate content of salmonberry (*Rubus spectabilis*) rhizome segments from the central Oregon Coast Ranges. Canadian Journal of Forest Research, 24, 272-277.

Zhou Y.H. and Wu B.S. (1997) Study on nutrient characteristics of the leaves of *Bambusa distegia*. Journal of Bamboo Research, 16, 13-18.

Zeigenfuss L.C., Singer F.J., Williams S.A. and Johnson T. L. (2002) Influences of herbivory and water on willow in elk winter range. Journal of Wildlife Management 66:788-795.